PLANT
FORM & FUNCTION

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PREFACE

We have in response to many requests combined in the present volume the substance of our two previous works, *An Introduction to the Study of Plants* and *An Introduction to the Structure and Reproduction of Plants*. In so doing we have not only endeavoured to bring the subject-matter completely up to date, but have slightly extended the scope. This has involved so many alterations, whether substantive or verbal, that the whole can almost be regarded as a new work. In particular, we may emphasise that, whilst the fundamental knowledge regarding morphology and anatomy has been fully presented, the physiological and ecological aspects have been materially extended. Economic applications have as before been emphasised. We may also call attention to the additional chapter on the British Flora and the introduction of brief accounts of additional families in the taxonomic section with the object of including all those to members of which frequent reference is made in the text.

The majority of the illustrations are original and are taken from our previous works, but over thirty figures have been added, and these embody more than a hundred new drawings and photographs.

The scope of the present work more than covers the first year University syllabus and should provide an adequate foundation for a non-specialised graduate course. To each of the more important sections there is appended a brief selected bibliography which is intended to serve as a guide to useful reference works (also listed under this heading in the index), where further information can be obtained.

We would stress that considerable care has been expended in the preparation of the Index in the belief that it will be found a real aid to the student.

We are indebted to Dr P. Haas for help in revising the biochemical sections, to Dr F. W. Jane for assistance with the sections dealing with cytology and for the preparation of figures illustrating these. We are also indebted for illustrations to Mr E. M. Cutting, Mrs F. E. Fritsch, Dame Helen Gwynne-Vaughan, Professor F. W. Oliver, Miss Pellew, and Miss E. M. Salisbury.

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London, *February* 1938.

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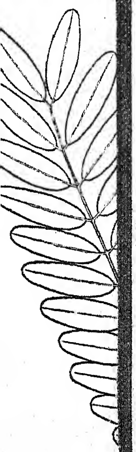

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CONTENTS

CHAPTER I

THE PLANT CONSIDERED AS A WHOLE

THE Vegetable Kingdom includes a great variety of simple and complex types and, in order to obtain a general idea of the living organism termed a Flowering Plant, the Shepherd's-purse (*Capsella bursa-pastoris*), which is exceptionally common on waste ground at all times of the year (Fig. 1), can be utilised. It soon appears on exposed soil that is not carefully tended, increasing very rapidly and successfully competing with other plants growing in the same situation, and thus possesses some of the distinguishing characteristics of a weed.

This, like all Flowering Plants, has a body consisting of two distinct parts which live under very different conditions. One part, the overground *shoot*,[1] comprising the stem bearing leaves (Fig. 1, *Sh.*), is surrounded on all sides by air and exposed during the daytime to the light of the sun. The other part, the underground *root* (Fig. 1, *Rt.*) is completely embedded in the soil and lives in darkness. The parts of the shoot (stem and leaves) are green, whereas the root and its branches are white. The branches of the root are all similar in appearance, but the stem bears different kinds of appendages, some of which are round and slender like itself, while others are flattened structures known as leaves.

Closer examination of the root shows that there is a main portion (Fig. 2, *m.a.*) which is a direct downward continuation of the stem, its position being therefore more or less vertical. This, the main axis of the root, bears side-branches (the *lateral roots*, Fig. 2, *l.r.*^{1}) which grow outwards and slightly downwards at an acute angle. In older plants the lateral roots bear further branches (Fig. 2, *l.r.*^{2}, *l.r.*^{3}) which spread out in all directions.

A short distance behind the tips of the main root and its branches careful examination with a lens may show a number of very short colourless hairs (the *root-hairs*) which, however, can be much more readily seen if a plant of the Shepherd's-purse, after washing away

[1] An important reference-book for plant-morphology is K. Goebel, *Organography of Plants* (translated by I. B. Balfour), 2 vols. Clarendon Press, 1900–1905 (3rd German Edition in 3 vols., 1928–33).

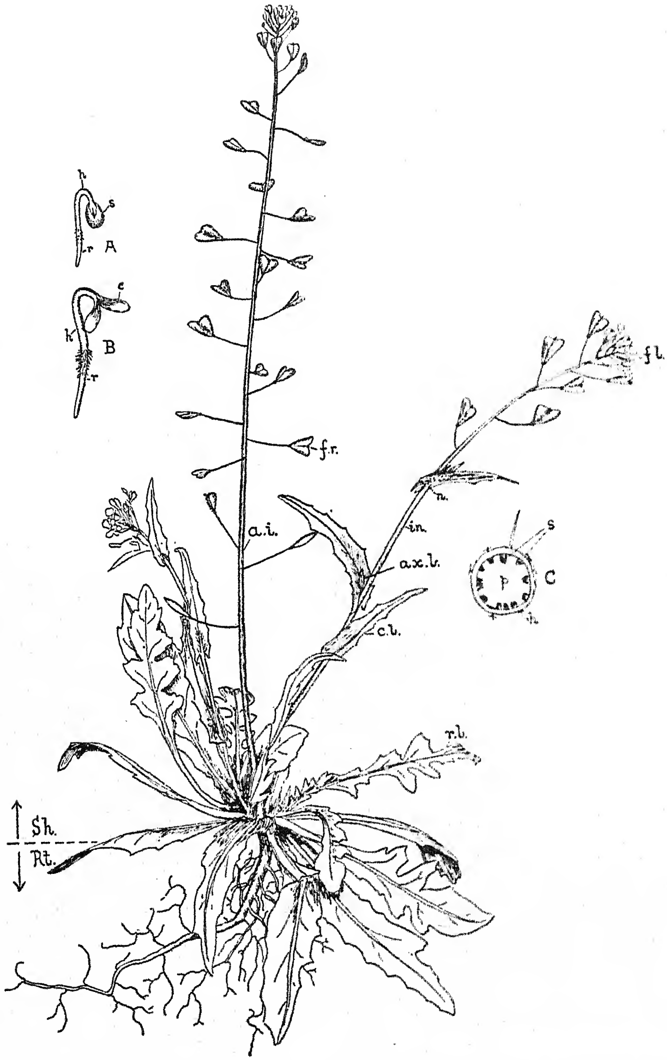

FIG. 1. Complete plant of Shepherd's-purse (*Capsella bursa-pastoris*) (slightly reduced). The surface of the soil is indicated by the dotted line on the left. *a.i.*, axis of inflorescence; *ax.b.*, axillary bud; *c.l.*, cauline leaf (see p. 119); *fl.*, flowers; *fr.*, fruit; *in.*, internode; *n.*, node; *r.l.*, radical leaf (see p. 119); *Rt.*, root; *Sh.*, shoot. A and B, Two stages in germination (somewhat enlarged). *c*, cotyledon; *h*, hypocotyl; *r*, radicle; *s*, testa. C, Cross-section of stem (magnified about 8 diameters). *h*, hair; *p*, pith; *s*, woody strands.

the soil, is placed for a day or two with its roots in water (Fig. 2, C, *r.h.*). In the root-system thus treated the extreme tips are seen to be devoid of root-hairs, each being protected by a darker hood-like covering, the *root-cap* (Fig. 2, C, *r.c.*) which is not readily discernible in a freshly uprooted plant. If the root be scraped with a

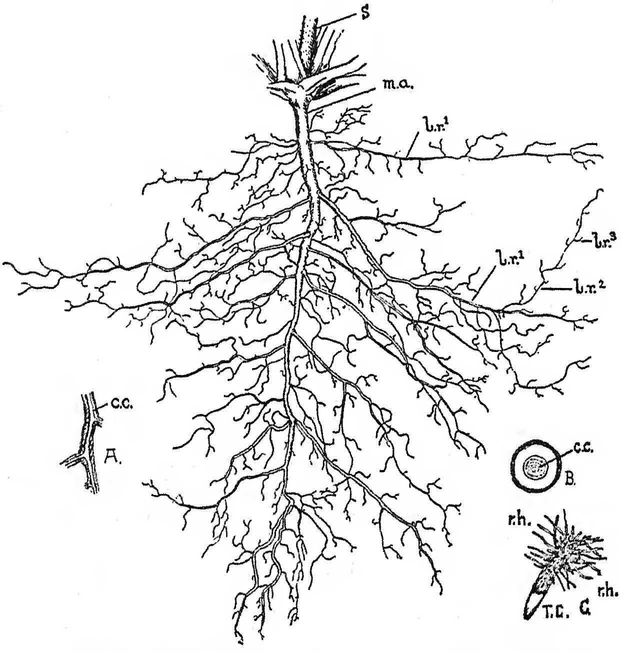

FIG. 2. Root-system of Shepherd's-purse (natural size). *S*, base of stem; *m.a.*, main axis of root; *l.r.*[1], lateral branches of first order; *l.r.*[2], laterals of second order; *l.r.*[3], laterals of third order. A, Longitudinal section through portion of main root (about 3 times natural size). B, Cross-section of same ($\times$ 9); *c.c.*, central core. C, Tip of a root grown in water ($\times$ 10). *r.h.*, root-hairs; *r.c.*, root-cap.

blunt instrument, the outer part is found to be soft, but, if the scraping be continued, a harder central core (Fig. 2, A and B, *c.c.*), which runs the whole length of the root, is revealed.

In the shoot, as in the root, we can distinguish a vertical main axis (Fig. 1, *a.i.*) bearing lateral branches which, however, grow outwards and upwards. All the lateral branches will be found to arise immediately above a leaf and, since the angle between a leaf and the stem upon which it is borne is termed the *axil* of the leaf (Fig. 3, E, *axil*), the branches are described as axillary (Fig. 1, *ax.b.*; Fig. 3, E, *a.b.*). That part of the stem from which a leaf arises is

called a *node* (Fig. 1, *n.*), whilst the portion between two nodes is spoken of as an *internode* (Fig. 1, *in.*). At the base of the stem a considerable number of leaves generally arise close together without perceptible internodes, forming on the surface of the ground a rosette (Fig. 1), which tends to die away as the plant grows older.

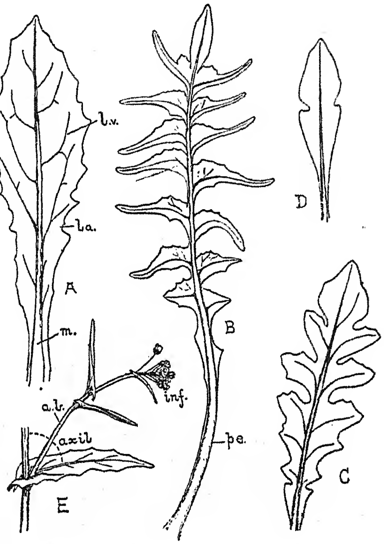

FIG. 3. A–D, Forms of radical leaves of Shepherd's-purse (about half natural size). *m*, midrib; *la*, blade; *l.v.*, lateral vein; *pe.*, petiole. E, Node with leaf and axillary branch bearing inflorescence (*inf.*) (about half natural size). *a.b.*, axillary branch.

By scraping away the surface of the stem, the soft outer part (*cortex*) is found to be quite a thin layer, and almost immediately we come to a number of narrow light-coloured strands consisting of harder substance and running lengthwise. On cutting across the stem these strands appear as a variable number of pale-green dots (Fig. 1, C, *s*) situated around the edge of the cross-section, whilst the central region is occupied by soft tissue (*pith*, *p*), a marked point of contrast to the root in this plant.

In the leaf two parts can usually be distinguished, the leaf-stalk or *petiole* (Fig. 3, B, *pe.*) and the flat *blade* or *lamina* (Fig. 3, A, *la.*). The margin of the latter is not regular, but, if we examine a number of plants, all types from leaves with an almost smooth outline to those in which it is deeply indented can be found (Figs. 1 and 3). In general the upper leaves are less deeply cut and have a shorter leaf-stalk than those forming the rosette—in fact, most of the upper leaves have no petiole at all (such leaves being described as *sessile*) and the base of their lamina forms two projections enclasping the stem (Fig. 1; Fig. 3, E). The lamina has an upper and a lower surface, of which the former is the darker green. Extending from the base to the tip of the leaf and forming a direct continuation of the petiole is a prominent strand, which projects markedly on the under side and is known as the *midrib* or principal vein (Fig. 3, A, *m*). Arising from the latter are a number of finer strands (the *lateral veins*, *l.v.*) which branch still further to form an incon-

spicuous network upon which the delicate substance of the blade is spread out.

The surfaces of stem and leaves bear numerous scattered *hairs* (Fig. 1, C, *h*). These outgrowths are of a white colour, and whilst some, especially prominent on the edges of the leaves, are simple and almost straight, others are branched in a star-shaped manner (Fig. 4, C).

Terminating the main stem and some of its larger branches are flowering shoots (*inflorescences*) consisting of small flowers borne on slender stalks (Fig. 1, *a.i.*; Fig. 3, E, *inf.*). Each flower is composed of the following parts (Fig. 4, A): On the outside there

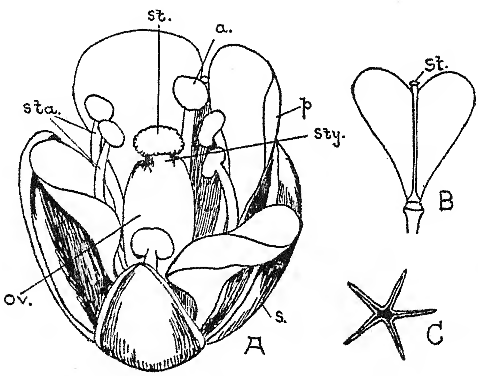

FIG. 4. A, Single flower of Shepherd's-purse (much enlarged); *s*, sepal; *p*, petal; *sta.*, stamens; *a.*, anther; *sty.*, style; *st.*, stigma; *ov.*, ovary. B, Single fruit (much enlarged); *st.*, stigma. C, Single star-shaped hair from leaf (much enlarged).

are four small greenish protective leaves, the *sepals* (*s*), collectively termed the *calyx*; next within, and alternating with the sepals, are four larger white *petals* (*p*), together known as the *corolla*; these are followed by six stamens (*sta.*), each of which consists of a short stalk or *filament* bearing at its tip a yellowish swelling or *anther* (*a*) containing a yellow powder, the *pollen*. In the centre of the flower is situated a small, green, flattened structure, the *ovary* (*ov.*), surmounted by a short peg-like projection, the *style* (*sty.*), which ends in a little sticky knob, the *stigma* (*st.*).

The pollen of the stamens is received by the stigma and, as a result of further growth, the ovary gradually develops into the ripe fruit (Fig. 4, B), during which the stalk of the flower elongates, calyx, corolla, and stamens wither away, and the internodes between the flowers lengthen (see Fig. 1). On older plants the ripe fruits are seen, in the lower part of the inflorescence, as flat green triangular

structures with an apical notch in which the remains of style and stigma can be distinguished (Fig. 4, B). Inside a ripe fruit we find a number of small brown bodies attached by short stalks, the seeds; these have developed from minute structures (the *ovules*), present in the ovary of the young flower, as a result of changes following upon the reception of the pollen by the stigma.

Older plants will show the ripe fruits opening of themselves and shedding the seeds, after which the parent sooner or later dies away. The seeds get washed into the soil by rain and after a brief period give rise to new plants. In this way the Shepherd's-purse not only reproduces its kind, but also multiplies.

Like most plants, the Shepherd's-purse is built up of innumerable small units called *cells*, the detailed structure of which can only be studied with a microscope. These cells are of various kinds, and have different functions. At the tips of the branches of root and stem are situated groups of very small cells, which during the growing period are constantly multiplying by division into two and thus providing the new units by means of which an increase in length takes place. These groups of cells are termed the *meristems*.

The purposes or functions of the different parts or organs may now be considered. It is obvious that the root primarily performs the function of fixing the plant in the soil, as shown by the effort which is often required to uproot it. The root-system offers considerable resistance to pulling strains, which is due to the central core of hard substance (p. 3). In the stem, on the other hand, the hard strands situated round the edge (cf. Fig. 1, C with 2, B) render it more suited to meet bending strains under the influence of the wind. The leaves which offer a relatively large surface to the wind would of course be particularly liable to become torn, were it not for the fact that the delicate tissue is fully supported by the network of the veins which, with the hard strands of the stem and root, form a continuous skeleton throughout the plant.

The second important function of the root is absorption of water from the soil, as witnessed by the rapid withering that ensues when an uprooted plant is left on the surface of the ground. The actual absorption of moisture can be demonstrated by placing a plant of the Shepherd's-purse with its root-system in a tumbler of water, the surface of the latter being covered by a thin layer of oil to prevent evaporation, and its level marked by a strip of gummed paper. A perfectly similar arrangement, but without a plant, should be set up beside it to serve as a control. After some hours the level of the water will be found to have fallen, whereas

no appreciable change is noticed in the control. In the intact root this absorption of water is actually effected by the root-hairs.

The stem, besides serving to bear the leaves and inflorescences, forms the channel through which the water absorbed by the roots is conveyed to the different parts of the shoot. By cutting off the tips of the roots of a complete plant and placing its root-system in an aqueous solution of light green (Appendix V), the whole course of the water through the plant can be traced. If, after some hours, we split up the main root and stem lengthwise, we shall find that the green colour is confined to the central core of the root and to the similar strands which run near the surface of the stem. Moreover, the veins of some or all of the leaves (and even parts of the flower) will be seen to be similarly coloured, thus proving that the continuous skeleton referred to above also serves as the water-conveying system of the plant.

The water which is thus brought to the leaves is not pure, but is a very weak solution of certain mineral substances present in the soil, and many of these are necessary for the nourishment of the plant. Of the moisture reaching the leaves a large volume escapes as water-vapour from the extensive evaporating surface which they present. This is easily demonstrated by the accumulation of moisture on the inside of a bell-jar placed over a healthy plant, although in order to obtain a reliable result both pot and soil should be covered with some waterproof material (*e.g.* tin-foil). The water retained is built up into the substance of the plant. The continual loss by evaporation is made good by absorption through the roots. A large quantity of water is absorbed, but the amount of mineral salts taken in is chiefly dependent on the extent to which they are built up or otherwise altered within the plant's body.

The process of evaporation from the leaves may be also roughly studied by using filter-paper soaked in a solution of cobalt chloride and subsequently dried. Such paper appears deep blue, but readily turns pink and finally almost colourless on exposure to moisture. Leaves are placed on a sheet of dry blotting-paper, some with their upper and some with their under surfaces directed upwards. Small pieces of the dry cobalt-paper are then laid on each, and the entire series is covered with a dry sheet of glass to prevent access of damp air. It will be noticed that the pieces of cobalt-paper in contact with the under surfaces of the leaves become colourless more rapidly than those upon the upper surfaces, thus showing that more water-vapour escapes in a given time from the under than from the upper side.

We shall find later that the surface-skin (*epidermis*) on both

sides of the leaf is perforated by a large number of minute pores (*stomata*) which are usually far more numerous on the under than the upper surface and whose size varies slightly at different times. The actual pores can be located by sealing up the cut end of the petiole with melted paraffin-wax and immersing the blade in warm water, when owing to the expansion of the air in the leaf the lower surface will become studded with numerous tiny air-bubbles, each marking the position of a stoma. The pores are commonly wide open in the light and almost closed at night, and it is through them that most of the water-vapour escapes. The rate of water-loss is dependent not only on external, but also on internal, conditions and therefore the process is distinguished from evaporation as *transpiration*. It is largely the increasing resistance to evaporation of moisture from the cells of the interior that checks this process, when too little water is supplied by the roots. When almost closed the stomata also effectively check transpiration, but in light they often remain open, even when the plant begins to wither. The reduced transpiration from a wilted as compared with a fresh leaf can be shown with the help of cobalt-paper.

The green colour of the leaves is due to a mixture of pigments known as *chlorophyll*, which are of importance in the nutrition of the plant. If a plant is killed by immersion in boiling water and is subsequently placed in alcohol, a solution of the chlorophyll is obtained, leaving the plant itself colourless. If some such leaves are now placed in a solution of iodine (Appendix V), they rapidly acquire a bluish-black colour which is a test for the presence of starch.

It can easily be shown that starch is only to be found in the leaves after the plant has been exposed for some time to the light. Two similar plants are grown in separate pots, the one in the light and the other in darkness. After forty-eight hours a leaf is removed from each plant and decolourised in the way described above. Treatment with iodine shows that starch is only present in the leaf from the illuminated plant.

If this experiment be continued, the plant in the dark assumes a starved appearance as compared with the one in the light, so that starch is evidently an important food-substance. Any new leaves formed in the dark are practically colourless, which shows that light is also necessary for the formation of chlorophyll. If a plant grown in the dark is subsequently exposed to illumination, it will be found that starch soon reappears in the green leaves, but no starch is produced in the colourless leaves until after they have become green. This shows that chlorophyll also is necessary for starch-production.

It will subsequently become apparent that the starch in the leaves of plants is formed, with the help of chlorophyll and the radiant energy of light, from the carbon dioxide of the air and some of the water which passes into the leaves, the air obtaining access to the interior through the stomata. Starch is a complex substance, a carbohydrate, composed of the elements carbon, hydrogen, and oxygen, and during its formation some oxygen is given off. The presence of carbon in starch can be demonstrated by strongly heating it in a dry test-tube, when most of the carbon remains behind as a black mass. The necessity of carbon dioxide for the production of starch can be shown by an experiment to be described later (p. 208).

The building up of starch and similar substances from carbon dioxide and water is sometimes spoken of as carbon dioxide assimilation, but, owing to the part which light plays in the process, the alternative term *photosynthesis* is now usually employed. This process is the first step in the nutrition of the plant and leads on to the formation of the more complicated substances of which it largely consists, and in the production of which the mineral salts absorbed from the soil play a part.

Another important vital process carried on by the plant involves the taking in of oxygen and the giving out of carbon dioxide. This is the *respiration* common to plants and animals. The exchange of gases is just the reverse of what occurs in photosynthesis, but this latter being a much more active process, respiration is completely masked in the presence of light. Consequently a demonstration of the fact that green plants respire can most easily be obtained in the dark. To show the need for oxygen soaked Peas are placed in a U-tube, one end of which is closed by a rubber cork. The U-tube is then inverted with the Peas resting on the cork and the other end is placed in a solution of pyrogallate of potash (Appendix V). The exposed surface of the solution is at once covered with oil. In the control, water is used to replace the pyrogallate. Whereas the Peas in the control sprout, those in the other apparatus fail to do so, which we may attribute to the pyrogallate having absorbed all the oxygen from the air within the tube. Respiration, in fact, is just as essential for the existence of the plant as for that of the animal.

The substances requisite for the nourishment of the plant are thus obtained from two sources, viz. the soil and the air. The root fixes the plant in the ground and absorbs water which contains mineral salts in solution. Most of this water is given off in transpiration, but the remainder, together with the dissolved salts, is retained and contributes to the maintenance of the plant. Through

the agency of the chlorophyll in the presence of light chemical changes are brought about, which transform the carbon dioxide and some of the water into food-substances. These together with their further products not only serve for the nourishment of the plant, but supply the material for continued growth. In this way the seedling, living at first on food stored within the seed, is able to increase in size and finally to form seeds, capable of giving rise to new individuals. All of these vital processes involve a loss of energy, supplied by the energy set free in respiration, and hence its importance for the maintenance of life.

CHAPTER II

PLANT-HABIT AND DURATION

THE life-history of many common plants is compassed in a single year. Some of these (Petty Spurge; *Tropæolum*) circumvent the cold season by dying away in the autumn, leaving only their seeds. These may be termed *summer annuals*, but there is another kind of annual that germinates in the autumn and is able to survive under winter conditions, though it dies with the coming of the summer; such *winter annuals* are exemplified by the annual Buttercup and the annual Forget-me-nots (*Myosotis*). There are some plants, particularly weeds like the Shepherd's-purse (Fig. 1) and the Groundsel (*Senecio vulgaris*), in which the whole life-cycle occupies a much shorter interval of time, so that several successive generations may be produced in a year. Owing to their rapid growth such plants readily establish themselves on disturbed soil. In some annuals the period from sprouting to seed-production does not exceed a few weeks.

The annual uses up all of its available food-materials in the production of seeds, but if this be prevented by removing the flower-buds as they appear, it may often be induced to survive for two or more seasons. There are, however, a large number of plants which in nature normally utilise more than a single year to amass the food-materials necessary for seed-formation. Some of these, which are termed *biennials*, flower only in the second year of their life and soon afterwards perish; examples are furnished by the Mullein (Fig. 5), Canterbury Bell (*Campanula*) and the Carrot. Such plants during the first season's growth do not get beyond the production of a basal rosette (Fig. 5, B). The food-substances formed by these leaves pass into the subterranean portion, which becomes somewhat swollen and serves as a storage-organ (Fig. 65, A, p. 113). During the ensuing winter the leaves, since they lie in close proximity to the soil, obtain a certain amount of protection by surrounding vegetation and inequalities of the surface of the ground. In the following year rapid growth takes place, largely at the expense of the food stored up in the underground parts, and

as a result a tall stem bearing numerous flowers is produced (Fig. 5, A). Under certain circumstances, such as growth on very poor soil, the biennial may form a few flowers and seeds already in the first year and then die away, thus behaving like an annual. The "bolting" of Cabbages, Onions, etc., in their first season is a comparable phenomenon due to complex physiological causes, in which temperature-changes often play a considerable rôle.

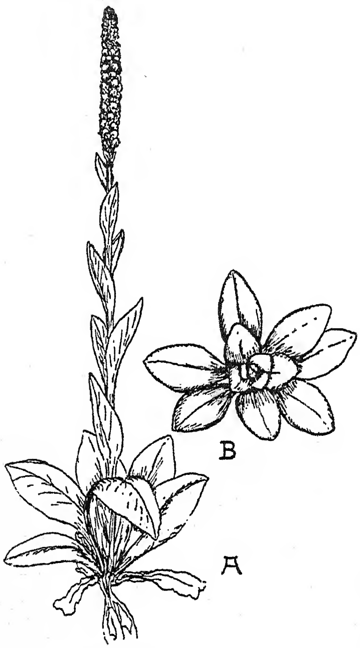

FIG. 5. The Mullein (*Verbascum thapsus*), a biennial (greatly reduced). B, rosette stage (first year). A, second-year stage.

We can readily imagine a biennial in which the vitality of the plant is not completely exhausted by the production of flowers and fruits, so that sufficient food-material remains to support renewed growth in the following spring. If this goes on from year to year we should obtain a so-called *perennial*, and a large number of plants in nature persist in this manner. Instances are the Stinging-nettle (*Urtica*), the Perennial Sunflower, and the Potato (Fig. 143, B, p. 228). If perennials are grown from seed, some flower already in the first year, whilst most require two or even more years[1] to attain to sufficient maturity before flowers are produced; meanwhile they are accumulating a store of food in their underground organs (Figs. 142 and 143, A, pp. 227, 228).

In the examples above mentioned the aerial parts die down at the end of each season, whilst the subterranean parts persist and by virtue of their store of food-material rapidly produce new shoots in the following spring. When the plant begins to form flowers, it is sufficiently vigorous to provide the necessary food for the resulting seeds, and yet to transfer enough into the underground organs for the commencement of next year's growth. A few perennials of this type, such as the Dandelion (*Taraxacum*) or *Iris*,

[1] There are some long-lived perennials which are like annuals in the fact that they only fruit once and then die (*e.g.* Talipot Palm, *Corypha*).

always retain some of their leaves even during the winter, and the same is true of most Grasses (winter-green perennials). Such plants, which lose part or all of their foliage for a period, form new leaves or lose them at very varying times.

The kinds of perennials hitherto noticed are called herbaceous perennials, since they produce no permanent overground shoot-system. In contrast to these, however, a large number of perennials, namely shrubs and trees, form stems which become hard and woody and persist to form the starting-point for each year's growth, a feature that enables some to attain very considerable dimensions. In the British flora such *woody perennials* are confined to one of the two great subdivisions of Flowering Plants, the so-called Dicotyledons (cf. p. 27), although this habit is also found among the Conifers (*e.g.* Scot's Fir, Yew, etc.). Even in these some part, as a general rule, dies back on the approach of winter, as is seen in the falling of the leaves of plants like the Beech, Hawthorn, etc., which are consequently described as *deciduous*.[1] A few others, such as the Holly and the Scot's Fir, are *evergreen*, bearing leaves throughout the year.

The store of food in these woody perennials is laid down throughout the woody portion of the plant and is here again responsible for the rapid sprouting which takes place with the advent of spring. Trees are essentially distinguished by their greater height and their frequent possession of a single main trunk.

The form of food-reserve in perennial plants is commonly starch, a fact which may be easily verified by cutting open the underground stem of the Iris or Crocus or a thick branch of the Horse Chestnut in winter, and applying the iodine-test (see p. 8). In other plants (*e.g.* Solomon's Seal and Dandelion) forms of food-material not giving this reaction are found (cf. Chap. VIII.).

The fact that so many plants die back on the approach of winter suggests that this may be related to the onset of colder weather. During winter the temperature of the soil is often so low that absorption of water by the roots practically ceases. If, under these circumstances, the plant were to lose water in transpiration (p. 8) at the same rate as in the warmer period of the year, it would soon wither and die. This evil is, however, avoided by the shedding of the leaves or the dying away of the whole overground shoot-system whereby the transpiring surface is greatly reduced. At first sight the evergreen would appear to be an exception to this rule, but it will be noticed that all evergreen

[1] For the derivation and meaning of this and other terms applied to plant-structures, see B. D. Jackson, *A Glossary of Botanical Terms*. 4th edit., Duckworth, 1928 (481 pp.).

leaves (*e.g.* the Laurel and the Holly) are of a leathery texture, due to an unusually thick epidermis. As a consequence, transpiration from such leaves goes on slowly at all times of the year, and such little absorption as occurs during the winter is sufficient to obviate severe wilting. It is instructive in this connection to compare the relative rates of transpiration of a deciduous and an evergreen leaf by the aid of the cobalt-method (p. 7).

Plants exhibit a number of diverse habits, of which the erect is by far the most frequent; in this type the aerial shoot-system is so

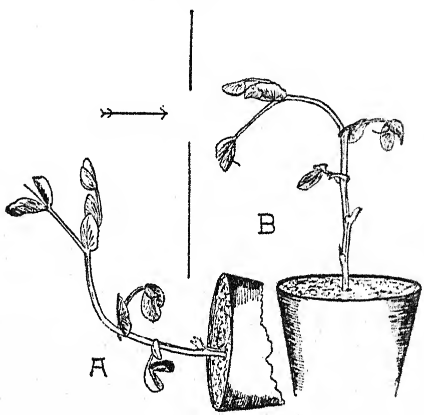

FIG. 6. A, Seedling of Pea, placed horizontally in the dark, showing the shoot bending up under the influence of gravity. B, Ditto, placed vertically and showing a phototropic curvature under the influence of one-sided light, whose direction is indicated by the arrow. (About one-third natural size.)

constructed as to be able to support itself. It is natural to ask why these plants maintain the erect position in nature. If an erect plant be placed next to a window, so that it receives one-sided illumination, the shoot will soon be found to have curved over towards the light (Fig. 6, B). When this has occurred the plant should be turned round through half a circle, whereupon after a further interval the shoot will again bend over towards the window. The erect growth of the stem is dependent on its being exposed to equal illumination on all sides, and one-sided light leads to a bending until equilibrium is again established. The influence of light upon the direction of growth of the plant is spoken of as *phototropism* (*heliotropism*).

It is not difficult to show that other influences play a part in determining the erect position of the shoot, for if we place a plant horizontally in the dark for some hours the tip of the shoot gradu-

ally curves upwards till it again assumes a vertical direction (Fig. 6, A); the same thing may be frequently observed in nature, when a plant is blown over by the wind, or a branch sinks down as a result of its own weight. In the plant placed in darkness some agency other than light is evidently at work and, as will be shown later, this is gravity which here has the peculiar effect of causing growth in a direction opposite to that of the gravitational pull. The influence of this force on the direction of growth is termed *geotropism*.

A word or two may be added on the advantages of the erect habit. In the first place, the leaves are thus well exposed to the light and most suitably placed for photosynthesis (p. 9). In addition, the flowers are displayed to the best advantage, a point of great importance, since many plants depend upon insects for the transference of the pollen from the stamens to the stigma. Moreover, the consequent height above the ground greatly facilitates the dispersal of the seeds when, as is frequently the case, this depends upon the action of the wind.

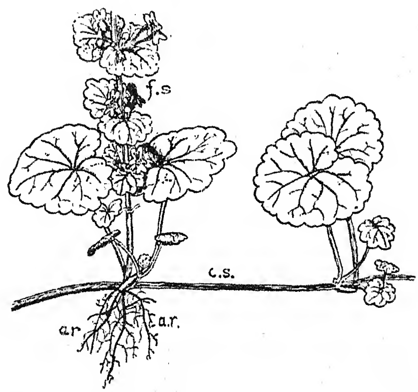

FIG. 7. Creeping stem (*c.s.*) of the Ground Ivy (*Nepeta glechoma*), showing adventitious roots (*a.r.*) and an erect flowering shoot (*f.s.*) (about half the natural size). The flowering shoot is not shown at its full length.

In marked contrast to erect plants are those which assume a creeping habit, as, for example, the Creeping Jenny (*Lysimachia nummularia*) and the Marsh Pennywort (*Hydrocotyle*). In these the influence of light and gravity on the direction of growth of the shoot must obviously be a different one. The main advantage of this habit lies in the rapidity with which the plant can cover a considerable surface, whilst the close proximity to the soil entails less exposure to atmospheric extremes. On the other hand, such plants run the risk of being overshadowed by surrounding vegetation and forego all the advantages which the erect habit brings with it. These drawbacks are to some extent minimised in certain creeping forms (*e.g.* the Ground Ivy, Fig. 7) by the production of erect flowering shoots from the axils of the leaves of the creeping stem.

There are still other plants which have the tendency to grow

erect, but after reaching a certain size fail to maintain this position unless they find some additional means of support which in nature is generally furnished by the surrounding vegetation. These *climbers* exhibit diverse methods of utilising such aid The simplest type is afforded by plants like the Goose-grass (Fig. 8, A), the Dog-rose (Fig. 8, B), and the Bramble (Fig. 140, p. 225), which grow vertically for a short time and then, bending over under their own weight, find a suitable support usually in the taller-growing shrubs round about. The apex of such a *scrambler* always tends to grow vertically upwards under the influence of light and gravity but, in the absence of any prop, the stem sooner or later falls on to the ground after which the younger portion again turns upwards; this is repeated until some

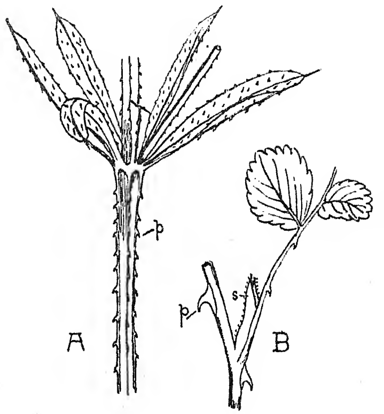

FIG. 8. A, Portion of shoot of Goose-grass (*Galium aparine*) (natural size), to show the prickles (*p*). B, Dog-rose (slightly reduced), with prickles (*p*) on stem and leaf (only a portion of the latter is shown). *s*, stipules.

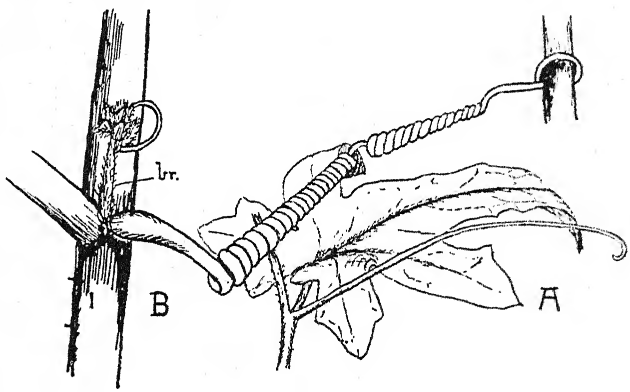

FIG. 9. Tendrils of the White Bryony (*Bryonia dioica*) (natural size). A, before, B, after clasping the support. *br.*, branch.

support is found, whereupon the erect part of the stem, in the course of its further growth, is raised above the surface of the

soil. The shoot in these plants is provided with curved prickles (Fig. 8, *p*), all of which have their tips directed downwards, so that the plant becomes hooked on to its means of support. In the Bramble and Dog-rose (Fig. 8, B) these structures are very conspicuous, but in the Goose-grass (Fig. 8, A) they are much smaller. Many weak-stemmed plants (*e.g.* the Stitchwort, *Stellaria holostea*), which grow more or less erect when they occur in masses, frequently behave as scramblers, if opportunity serves, but do not possess any very marked equipment for this purpose.

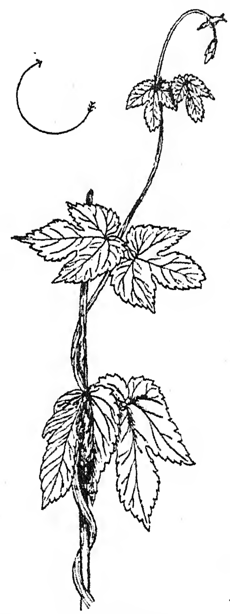

FIG. 10. Twining stem of Hop (*Humulus lupulus*) (about half the natural size), showing small leaves and long internodes of apical portion. Direction of twining indicated by the arrow.

More specialised climbers are those which develop *tendrils*, such as the Sweet-pea (Fig. 169, B, p. 264) and the White Bryony (Fig. 9). These tendrils appear as thin naked green stalks (Fig. 9, A) which, on contact with a branch or twig, twine round it (Fig. 9, B) and in this way the plant, as it grows, becomes attached to its support (cf. Chapter XXIV).

A third method of climbing is adopted by those plants in which the stem itself twines around the supporting object, as in *Convolvulus* and the Hop (Fig. 10). The shoot here at first grows erect, but after attaining a certain height the tip bends over and revolves in a circle (as indicated by the arrow in Fig. 10), a movement which helps the plant to find an object around which to coil. In these *stem-twiners* the apex of the shoot bears very small leaves (Fig. 10), which soon become separated by remarkably long internodes. As a result of this, twining is accomplished before the leaves are sufficiently large to interfere materially with the encircling of the support. In the Hop the grip of the climbing stem is greatly aided by the presence of curved prickles similar to those of the scramblers above considered. The Ivy is unusual in climbing by means of roots (Fig. 61, p. 109).

The end attained by the climber is the same as in the erect plant, viz. the exposure of its leaves to adequate illumination, the display of its flowers in a conspicuous position and the placing of its fruits in a situation aloft suitable for seed-dispersal. This type of habit is in nature found more particularly amongst the dense vegetation

of hedges (Fig. 11) and thickets, where competition is keen and adequate means of support are available, typical instances being

FIG. 11. Photograph of foot of hedgerow, taken close at hand. *b*, White Bryony; *c*, Chickweed; *g*, Goose-grass; *s*, Stinging Nettle.

furnished by the Honeysuckle and the Black Bryony. The climber enjoys the advantage of being able to dispense with so elaborate a supporting skeleton as that required by the ordinary erect plant, and the material thus economised can be used for rapid growth and the formation of abundant flowers and seeds; on the other hand, its existence turns on the finding of a suitable support and, if this fails, it has little chance of surviving.

Plants of a particular habit are often characteristic of certain situations, climbers of the hedgerow, rhizomatous plants (p. 226) of shifting soils, perennials of cold regions, short-lived annuals of tropical deserts, and annuals of cornfields or other disturbed soil. It is important to recognise that the air becomes drier and the speed of the wind greater with the height above ground. As a consequence the lower the stature of a plant, the less it is exposed to extreme conditions. It will be realised therefore that the level, at which the perennial parts of the plant occur, is a feature of importance; the buds of trees are more exposed than those of shrubs, those of Creeping Jenny which rest on the surface of the ground are less protected than the buds of

Dog's Mercury (*Mercurialis*) which occur just below it, whilst the resting stem of the Cuckoo-pint (*Arum maculatum*) which is often 8 inches under the ground is still better shielded. But the lower the stature of a plant, the less its capacity to compete for light.

This brief review of the various types of plant-habit shows that each has its own advantages, especially in relation to the conditions which obtain in nature. Form and duration are always subservient to the adequate nourishment of the individual, its reproduction and consequent multiplication. Advantages on the one hand are, however, balanced by disadvantages on the other. Thus, if the perennial be able to produce numerous seeds year after year, it also requires a relatively long period of preparation. An apple tree raised from a pip, for example, rarely bears fruit before it is seven years old. Most woody perennials therefore tend to disappear where browsing animals are plentiful, and so it is that with increase of population woody types tend to become replaced by herbs.

CHAPTER III

DICOTYLEDONOUS SEEDS AND SEEDLINGS

MOST Flowering Plants sooner or later produce fruits and seeds which represent the culmination of each season's growth. The seeds eventually come to lie on the rugged surface of the soil. By the action of the summer's heat and winter's frost the soil becomes broken up, and into the numerous crevices thus formed the seeds are washed by rain. Burrowing animals, especially earthworms, contribute to this process and, since in the course of their nutrition considerable quantities of soil are passed through their bodies and become deposited at the surface, they constantly transfer earth from below upwards, leaving corresponding spaces in the soil below. In rainy weather the little streams of water that percolate into the ground wash the seeds downwards, whilst at the end of each season's growth fallen leaves and other vegetable *débris* accumulate on the surface and thus afford added protection. In these various ways the seeds become buried at some slight depth in the soil.

In many plants the seeds remain dormant in the ground until the following spring, when conditions become favourable for *germination*. Seeds only germinate when provided with sufficient moisture, warmth, and adequate oxygen for respiration (cf. p. 9). In nature, the supply of water and oxygen are as a rule sufficient for germination, and it is often the low temperature of the soil that delays this process until the spring.

Many seeds, even if placed under suitable conditions, will not germinate immediately after being shed, but require a longer or shorter period of rest. In a number of plants which flower and form their seeds early in the season—*e.g.* the Field Speedwell (*Veronica arvensis*) and the Poppy—this dormant period is over by the late summer or autumn, and in such germination mostly takes place at this time of the year, the young plants remaining small and passing through the winter without appreciable growth (cf. p. 560).

Dormancy in seeds is a phenomenon dependent on various causes, of which the commonest is probably the difficulty with which water penetrates the coat of the seed. In many seeds with

comparatively impermeable coats, such as Sweet Peas or Lupins, abrasion of the seed-coat will hasten germination.

We may now study the outward characters of some common seed such as that of the Runner Bean (Fig. 12, A). It is more or less kidney-shaped and is covered with a smooth, tough skin, the seed-coat or *testa*. Along one of the edges of the seed there is a narrow white mark (the *hilum*, *h*) which is the scar where the seed was attached to the pod. At one end of the hilum are two minute swellings (*s*) side by side, whilst near the opposite end is a very small hole (the *micropyle*, *m*) situated at the base of a slight depression.

If some of these seeds be put to soak in tepid water a wrinkling of the seed-coat begins in the neighbourhood of the micropyle and gradually spreads over the whole surface. Still later the testa again becomes smooth, the seed having now increased to about double its original size. The explanation of these changes lies in the fact that water is first absorbed into the seed-coat at the micropyle and subsequently throughout the testa. Since the contents of the seed do not at this stage take up water nearly so rapidly, they show little increase in size, so that the enlarging testa is thrown into numerous folds. Subsequently the seed-contents also absorb water vigorously and swelling up gradually fill out and finally burst the surrounding testa. This swelling is accompanied by the exertion of considerable force, which can be shown by filling a narrow-mouthed glass bottle with dry Beans and placing it in a vessel of water; the seeds, as they swell, become more and more tightly packed, until eventually they burst the glass. This principle is, in fact, often employed for the purpose of removing dents in tin cans, etc.

For the examination of the seed-contents it is most convenient to use seeds which have been previously soaked, although the same features could be made out in the dry condition. On removal of the testa two cream-coloured fleshy lobes, the seed-leaves or *cotyledons*, are disclosed (Fig. 12, B, *c*). If the two cotyledons be carefully separated, a small bud bearing minute yellowish-green leaves (the *plumule* or primary shoot, Fig. 12, B, *p*) will be seen lying between them near to one edge. A close scrutiny shows that each cotyledon is attached to the base of the plumule by a very short petiole, whilst beyond this point the axis of the plumule is prolonged into a short tapering outgrowth, the *radicle* or primary root (*r*). Whereas the plumule is completely hidden between the cotyledons, the radicle after removal of the testa is seen as a projection lying against their edges (cf. Fig. 12, B). The young plant, found within the seed, is termed the *embryo* and includes three types of organs, viz. the radicle, plumule, and cotyledons.

The tip of the radicle fits into a short pocket which arises from

the inner surface of the seed-coat and ends near the micropyle. This pocket acts like the wick of a lamp in drawing up moisture from

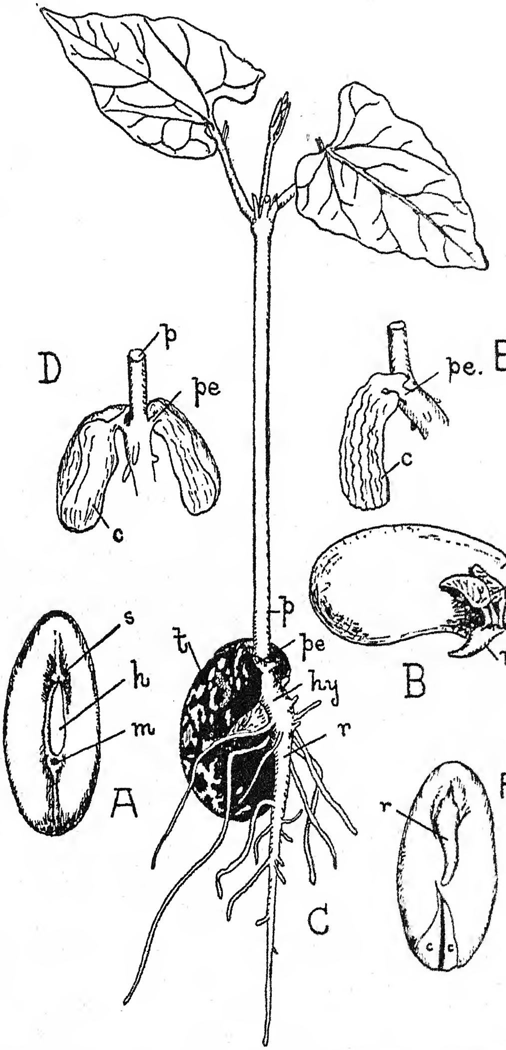

FIG. 12. Stages in the germination of the Runner Bean (*Phaseolus multiflorus*) (all natural size). A, Soaked seed seen edge on, to show the hilum (*h*), the micropyle (*m*), and the swellings (*s*). B, Seed with testa and one cotyledon removed to show plumule and radicle. C, Mature seedling. D, Partially shrivelled cotyledons, showing attachment to base of plumule. E, Ditto from side, with completely shrivelled cotyledon. F, First stage in germination. *c*, cotyledon; *hy.*, hypocotyl; *p*, plumule; *pe.*, stalk of cotyledon; *r*, radicle; *t*, testa.

the soil and passing it on to the radicle, so that this is the first part of the embryo to receive water and swell to a considerable size. As a result it is here that the pressure upon the seed-coat is most pronounced and that the bursting of the testa begins. The radicle, thus freed, grows rapidly downwards (Fig. 12, F) and very soon side-roots arise from it, so that the young plant becomes firmly anchored in the soil. In the meantime the stalks of the cotyledons are slowly increasing in length (Fig. 12, D, *pe*) and, since the cotyledons themselves remain firmly embedded in the seed on the one hand and the root is fixed in the soil on the other, this elongation has the effect of carrying out the plumule clear of the seed-coat (Fig. 16, A). Up to this time the plumule has altered little in size, but now a rapid growth in the upward direction begins. Until after the surface of the soil is reached, the tip of the plumule remains sharply curved, so that it is the more mature region that pushes its way through the ground dragging after it the young tender leaves at the apex (Fig. 16, A). The curvature rapidly straightens out after the plumule comes above the surface of the soil into the light (Fig. 12, C).

The early stages of germination are accomplished in darkness, and as a consequence the seedling is unable to manufacture food (cf. p. 9). The early growth of the embryo has in fact taken place at the expense of food-substances which became stored up within its cotyledons whilst the seed was still attached to the parent-plant. The bulk of this food consists of starch. If seedlings be examined at successive stages of germination, it will be seen that, as growth proceeds, the cotyledons shrivel up more and more (Fig. 12, D and E) until finally but a shrunken remnant is left. In the Runner Bean therefore the cotyledons are merely storehouses for nourishment.

An experimental demonstration of the great part played by the food-reserves in early stages of germination is furnished by carefully cutting off the cotyledons from a number of seedlings in which the radicles have obtained a hold upon the soil. A comparison of normal seedlings with those thus treated will show how great an asset this store of nourishment is to the plant (Fig. 13).

As a second example of a seed we may take that of the Castor Oil plant (Fig. 15, A). Neither the hilum nor the micropyle are visible on the testa (*t*), owing to their being covered by a warty outgrowth (the caruncle, *car.*), which arises late in development. By splitting the seed lengthwise in the plane of flattening and examining the exposed surfaces of the two halves a thin white leaf-like structure showing midrib and lateral veins will be seen on each (Fig. 15, B, *c*). These are the cotyledons which in this plant are very thin and only occupy a small portion of the seed-contents

(Fig. 15, C, *c*). On one or other half, at the narrower end of the seed, will be found a small white peg (Fig. 15, B), the pointed end of which lies nearest the caruncle and constitutes the radicle (*r*), whilst the opposite blunt end represents the plumule (*p*). The stalks of the cotyledons are here hardly recognisable.

The embryo of the Castor Oil seed, while showing the same

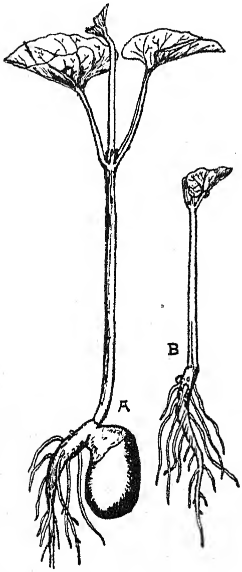

FIG. 13. A, Normal seedling of the Runner Bean. B, Seedling of the same age, from which the cotyledons were removed at an early stage of germination. (Both about half the natural size.)

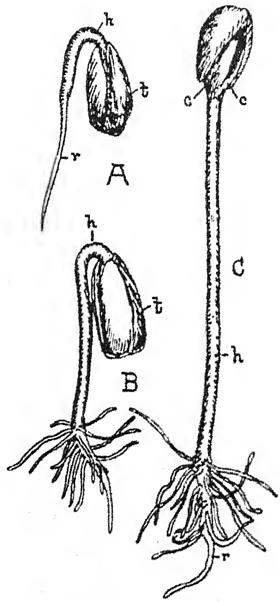

FIG. 14. Germination of Sunflower (*Helianthus*) (natural size). A, Showing escape of radicle and commencement of elongation of hypocotyl. B, Later stage. C, Hypocotyl straightened and cotyledons about to escape from the seed-coat. *c*, cotyledon; *h*, hypocotyl; *r*, radicle; *t*, combined fruit-wall and testa.

organs as that of the Bean, is thus much less developed in the resting condition. A further distinction is that the embryo of the Castor Oil only occupies part of the seed and that it is completely surrounded by a white fleshy mass, the *endosperm* (Fig. 15, B and C, *e*), which is all that one sees when the seed-coat is removed. This is a tissue containing food-reserves for the nourishment of the young plant, and the chief difference from the Bean is therefore that in the latter the food-substances are stored up *in the embryo itself*, whereas in the Castor Oil there is this special food-tissue

outside the embryo. Seeds which possess this tissue are said to be *endospermic*, whilst those lacking it (*e.g.* the Bean) are described as *non-endospermic.* Treatment with iodine shows that starch is not

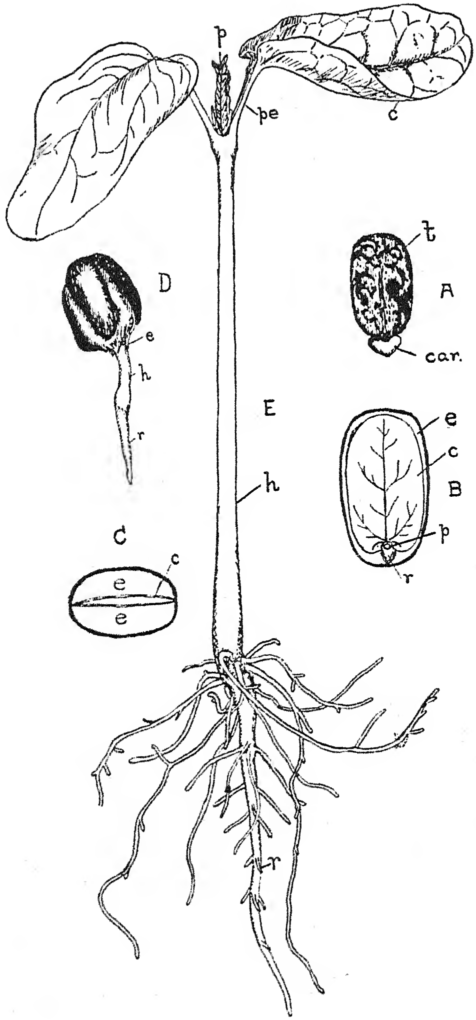

FIG. 15. Structure of seed and germination of Castor Oil plant (*Ricinus communis*) (A, D and E natural size, the others enlarged). A, Entire seed. B, The same halved lengthwise. C, Ditto, cut across. D, First stage in germination. E, Mature seedling. *c*, cotyledon; *car.*, caruncle; *e*, endosperm; *h*, hypocotyl; *p*, plumule; *pe.*, petiole of cotyledon; *r*, radicle; *t*, testa.

present in the endosperm of the Castor Oil seed, its place being taken by the oil which is used medicinally.

The first result of placing these seeds to soak is that the caruncle, which sucks up water like a sponge, increases in size and becomes softer. The seed-coat is so rigid that practically no swelling of the seed as a whole is observed and, since the water absorbed by the caruncle is passed on to the adjacent radicle, this part of the embryo is again the first to swell up, leading to a rupture of the testa at this point. The radicle grows downwards into the soil (Fig. 15, D) and begins to form lateral roots whereby, as in the Bean, the young plant becomes fixed. If a slightly older seedling be examined (Fig. 16, B), it will be noticed that prominent elongation is taking place in a region of the axis situated between the place of origin of the lateral roots and the point of attachment of the cotyledonary stalks. This elongating region has a reddish tinge in contrast to the white root and represents a portion of the stem situated *below* the cotyledons, for which reason it is spoken of as the *hypocotyl* (Fig. 16, B, *h*). Such a hypocotyl is present also in the Runner Bean (Fig. 16, A, *h*), but remains so short that it is difficult to recognise.

The rapid growth of the hypocotyl in the Castor Oil results in its becoming arched upwards (Fig. 16, B), and very soon the top of this arch appears as a loop above the soil. Subsequent to this the hypocotyl begins to straighten as a result of its further growth, and consequently the cotyledons, with the plumule enclosed between them, are dragged out of the ground (Fig. 15, E).

If a seed be examined a little time before the cotyledons emerge, the endosperm will be found to have nearly disappeared. During their long sojourn beneath the surface the cotyledons are occupied in absorbing food from the endosperm for the growth of the seedling, and throughout this period are undergoing a great increase in size, so that when they come above the ground they are many times larger than in the resting seed and have pronounced petioles (Fig. 15, E, *pe*). As the hypocotyl becomes erect the cotyledons spread out their green blades to the light (Fig. 15, E), and now serve as photosynthetic organs; subsequently the plumule forms other leaves and the cotyledons drop off.

The method of liberation of the plumule from the seed is obviously quite different in these two examples (cf. Fig. 16), for, whilst in the Runner Bean this is effected by elongation of the cotyledonary stalks, in the Castor Oil it is the lengthening of the hypocotyl that fulfils this purpose. In both seedlings the delicate tip of the plumule does not push its own way through the soil, the pressure of the soil being received either by the older part of the

plumule or by the hypocotyl; in the Castor Oil the risk of injury by friction with the soil-particles is still further reduced owing to the inclusion of the plumule between the cotyledons during its passage through the ground. Another difference between Runner Bean and Castor Oil lies in the behaviour of the cotyledons, since in the former they remain permanently underground and are said

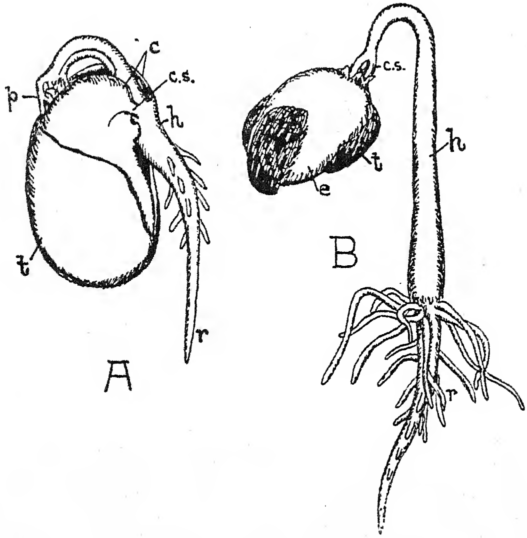

FIG. 16. Liberation of plumule in A, the Runner Bean; B, the Castor Oil (about natural size). *c*, cotyledons; *c.s.*, cotyledon-stalk; *e*, endosperm; *h*, hypocotyl; *p*, tip of plumule; *r*, radicle; *t*, testa.

to be *hypogeal*, whilst in the latter they eventually appear above the surface and are termed *epigeal*.

The two types of seed-structure and germination described in this chapter are characteristic of a large number of Flowering Plants which, owing in part to their possession of embryos with two cotyledons, are grouped together under the name of Dicotyledons. As further examples of non-endospermic Dicotyledonous seeds with hypogeal cotyledons we may mention the Pea and the Acorn, but there are also non-endospermic seeds with epigeal cotyledons, as, for instance, the French or Kidney Bean (*Phaseolus vulgaris*), the Shepherd's-purse (Fig. 1, A and B), and Sunflower (see Fig. 14); the cotyledons here remain within the seed until most of their food-material has been absorbed. Endospermic seeds may have either hypogeal or epigeal cotyledons; the former are very rare amongst Dicotyledons, whilst examples of the latter are furnished by the Castor Oil and the Buckwheat (*Fagopyrum*). The dry fruit of the

latter has three prominent ridges and exhibits, at the broader end, the remains of the floral leaves. When cut across the middle, the white endosperm is seen occupying the greater part of the interior, whilst the cotyledons appear as an irregular yellowish line. If cut lengthwise, the body of the embryo may also be seen towards the pointed end of the fruit, with the radicle directed outwards. Here, too, the cotyledons are recognisable as a wavy line. Since the hypocotyl is mainly responsible for bringing the cotyledons above the surface of the soil, it is always well developed in epigeal seedlings, whilst in the hypogeal types it generally remains short.

CHAPTER IV

MONOCOTYLEDONOUS SEEDS AND SEEDLINGS

A LARGE number of Flowering Plants, of which the Grasses, the Lilies, and the Palms furnish examples, possess embryos having but a single cotyledon. For this and other reasons such plants are grouped together as Monocotyledons and with the Dicotyledons form the two great subdivisions of Flowering Plants. Apart from the difference in the number of cotyledons, however, the embryo of Monocotyledons shows a similar structure to that of Dicotyledons, and both non-endospermic and endospermic seeds are found, although the latter type is by far the most common.

As a first instance of a Monocotyledonous seed we select the grain of the Maize owing to its large size, but any one of the Cereals (*e.g.* Wheat, Barley, Rye, etc.) would on a smaller scale show the same essential structure and mode of germination. In the dry grain (Fig. 17, A), one end, the former point of attachment to the cob, is more or less tapering whilst the other is broad and rounded, two sides of the grain being generally somewhat flattened. On one of these flat faces a whitish oval depression (*e*) marks the position of the embryo, the remaining yellow part of the contents of the grain consisting of endosperm. Above that end of the oval depression which lies remote from the scar of attachment of the grain, careful examination will reveal a second scar-like projection, the remains of the stigma (*st.*). This shows that the grain of the Grass is still enclosed in the ovary-wall and therefore really represents a fruit containing a single seed. The seed-coat is joined up with the surrounding ovary-wall (cf. p. 474), so that the two cannot be readily distinguished from one another, and as a consequence the micropyle cannot be seen. A little above the middle of the white patch caused by the embryo, at the end nearest the stigma-scar, a shallow and slightly darker depression, marking the position of the plumule, is frequently recognisable.

After removal of the envelope from a soaked grain, the white embryo and the yellow endosperm are readily distinguished. A faint line runs vertically up the face of the exposed embryo. By

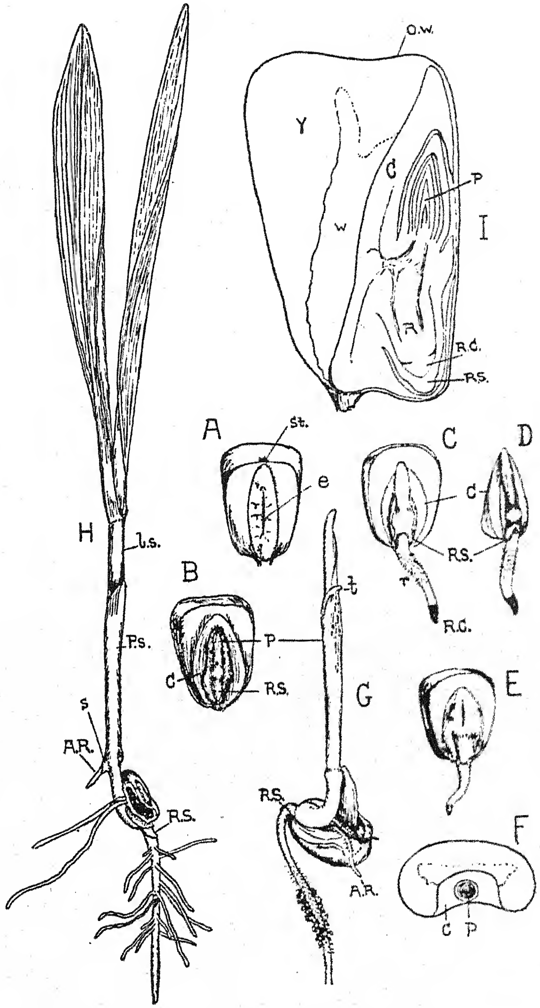

FIG. 17. Structure of grain and germination in the Maize (*Zea mais*) (all figures slightly enlarged, I × 8). A, Entire grain showing outline of embryo. B, Grain with envelope removed and edges of cotyledon folded back to show plumule and radicle. C, Early stage in germination, envelope removed. D, Embryo of same, dissected out. E, First stage in germination. F, Cross-section of grain with envelope removed. G, Late stage in germination showing escape of foliage-leaves from sheath. H, Mature seedling. I, Longitudinal section of complete grain (much enlarged). *A.R.*, adventitious roots; *c*, cotyledon; *e*, embryo; *l.s.*, leaf-sheath; *O.W.*, ovary-wall; *P*, plumule; *P.s.*, coleoptile; *R*, radicle; *R.C.*, root-cap; *R.S.*, root-sheath; *S*, sheath round base of adventitious roots; *St.*, stigma; *t*, tip of coleoptile; *W*, starchy endosperm; *Y*, flinty endosperm.

cutting a shallow slit along this line with the extreme point of a penknife and turning back the two edges of the cotyledon (Fig. 17, B), two peg-like projections are revealed, one directed towards the original point of attachment of the grain and representing the radicle (*R.S.*), the other placed in the opposite direction and constituting the plumule (*P*). The remainder of the white embryo comprises the single large cotyledon (*c*) which is wrapped round both plumule and radicle.

A further insight into the structure of the embryo is obtained by halving the peeled grain lengthwise along the same faint line as before (Fig. 17, I). The embryo is then seen to occupy the whole of the base of the seed, but tapers off to one side above, whilst the cotyledon (*c*) lies in close contact with the endosperm. The short blunt radicle (*R*) (terminated by a darker root-cap, *R.C.*) is now easily recognised and is seen to be enclosed in a special cap-like sheath, the *root-sheath* (*R.S.*, also seen in Fig. 17, B), whilst the plumule (*P*) consists of the central meristem encased in a succession of sheathing leaves (see also *P* in Fig. 17, F). From one side of the axis of the embryo, where plumule and radicle join, the large shield-shaped cotyledon (*c*) arises on a short thick stalk. The whole margin of the cotyledon is drawn out, so as to surround the rest of the embryo (see Fig. 17, F), leaving a slit-like aperture opposite the plumule. Careful examination with a lens shows that the root-sheath and the outermost sheath of the plumule both arise near the point of attachment of the cotyledon.

Around the former point of attachment of the grain is some whitish chaff (representing remains of the Maize flower) which probably facilitates the absorption of water, but the soaked grains of Maize exhibit but a slight increase in size as compared with dry ones. The radicle is again the first part of the embryo to receive water and the first to emerge, bursting through the skin of the grain and growing down into the soil (Fig. 17, E); around its base the split root-sheath can be plainly distinguished (*R.S.* in Fig. 17, C and D). The emergence of the radicle is very soon followed by the outgrowth of the plumule, which pierces the skin by its *own active growth* and pushes its way to the surface (Fig. 17, C and D). The radicle does not grow into a sturdy main root as in the Bean or Castor Oil, but is almost immediately followed by a number of similar roots (Fig. 17, G, *A.R.*), developing near the base of the radicle; these adventitious roots are sometimes recognisable already before germination and often grow more vigorously than the primary one which is soon indistinguishable from them.

The plumule, unlike that of the Dicotyledonous seedlings, remains straight during its passage through the soil, but the soft

meristem and the young leaves encasing it are nevertheless amply protected by the outermost sheath (*coleoptile*), the tip of which (*t* in Fig. 17, G) is hard and pointed. It is thus again a structure (viz. the tip of the outermost sheath), already matured within the seed, that has to endure friction with the particles of the soil. On reaching the surface of the ground the sheath becomes exposed to the light and the inner leaves of the plumule burst through (Fig. 17, G and H). In these foliage-leaves we can distinguish two parts, the narrow green blade and a paler portion (the leaf-sheath) which fits closely around the stem (Fig. 17, H, *l.s.*). The coleoptile, having served to protect the plumule whilst piercing the soil, remains as a sheath around the base of the stem (Fig. 17, H, *P.s.*), differing only from the later leaves in the absence of a blade.

During the whole process of germination the cotyledon remains underground within the seed and is actively absorbing nourishment for the growing embryo from the adjacent endosperm. Two regions are distinguishable in the latter, the portion nearest the embryo being white and relatively soft, whilst the remainder is yellow and harder (Fig. 17, I, *W* and *Y*). If we halve a grain lengthwise, the white portion will alone give the starch-reaction with iodine; the remainder of the endosperm consists of thick-walled tissue. In the Sweet Corn the starch is replaced by sugar. As in the Castor Oil, the reserve material will be found to have diminished in grains attached to older seedlings.

The Onion will serve as a second example of a Monocotyledonous seed. In the dry condition this is a more or less wrinkled structure, with three irregular faces and provided with a black testa (Fig. 18, A), one of the edges being prominently concave. If a number of seeds are cut lengthwise, so that the plane of section passes through the concave edge and the opposite face, it will be seen (Fig. 18, B) that, apart from the testa, the seed consists of a mass of greyish-white endosperm (*e*) containing near the margin a whitish coiled embryo; the latter appears to be a uniform structure, but in fact consists of a radicle (R), grading over imperceptibly into the cotyledon (*c*) which completely ensheathes the plumule.

Owing to the hard testa there is no appreciable increase in size when the seed begins to take up water. The first evidence of germination (Fig. 18, C) is as usual the appearance of the radicle (*R*) at one end of the seed, and this is followed by elongation of the embryo as a whole (Fig. 18, D). The green colouration which is rapidly assumed by the part nearest the seed now distinguishes the cotyledon (*C*), the tip of which remains embedded within the endosperm, from the white radicle (*R*). In the course of its further elongation the cotyledon becomes prominently arched, this arch

being retained for a considerable period, and by its continued growth in the upward direction the seed is often raised considerably above the surface of the ground (Fig. 18, E). At this stage the base of the cotyledon exhibits a slight swelling owing to increase

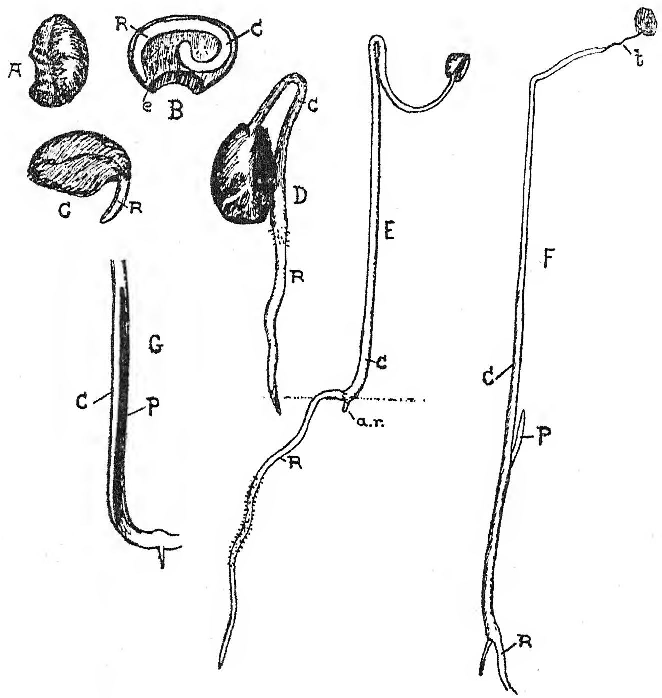

FIG. 18. Structure of seed and early stages of germination of the Onion (*Allium*) (A–D and G considerably enlarged, E and F about twice natural size). A, Entire seed. B, Seed halved lengthwise to show embryo and endosperm. C, Emergence of radicle. D, Elongation of cotyledon. E, Older seedling showing swelling at base of cotyledon due to plumule. F, Appearance of plumule and withering of cotyledonary tip. G, Longitudinal section of base of cotyledon in stage E, to show contained plumule. *a.r.*, adventitious root; C, cotyledon; *e*, endosperm; *P*, plumule; *R*, radicle.

in size of the contained plumule, whilst adventitious roots frequently develop just below this level (Fig. 18, E, *a.r.*). Finally the plumule bursts through the cotyledonary sheath (Fig. 18, F) and commences to unfold its leaves.

Throughout germination the tip of the cotyledon remains within the seed, serving to transfer the food-materials from the endosperm to the growing plant. In late stages, such as that seen in Fig. 18, F, the seed is found to be almost empty and, on cutting

3

it in half, shows apart from the withered tip of the cotyledon only shrivelled remnants of the endosperm. The cotyledon functions, then, in the same way as that of the Maize, but whereas in the latter the entire structure is employed for purposes of absorption, in the Onion the larger part emerges from the seed, becomes green and not only serves as a photosynthetic organ, but also constitutes the means of liberation of the plumule. The Onion thus exhibits a fourth type of germination shown by many other Monocotyledons, *e.g.* Lily, Date.

We have seen that water is a prime necessity for germination,

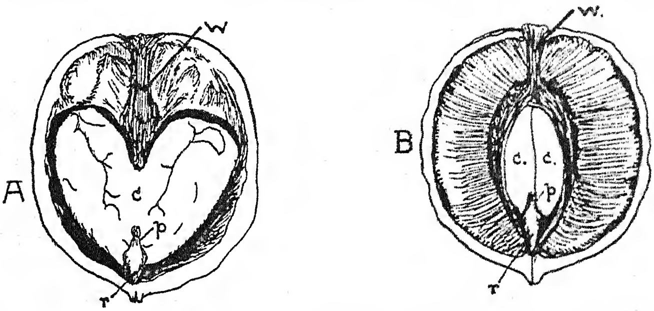

FIG. 19. Structure of the Walnut (*Juglans*) (natural size). A, Section cut lengthwise *between* the two halves of the shell. B, Section cut lengthwise at right angles to the plane of A. *c*, cotyledon; *p*, plumule; *r*, radicle; *W*, wick-like strand.

and that, in order to facilitate its absorption, many seeds are provided with definite mechanisms (*e.g.* the pocket of the Bean, the caruncle of the Castor Oil, etc.). A still more striking example is furnished by the Walnut (Fig. 19), which, when halved longitudinally, shows a prominent wick-like strand (*W*), running from one end of the nut to near its centre and terminating some little distance from the tip of the plumule (*p*). The water diffuses through this strand and from it passes into the thin membranous plates lying between the lobes of the cotyledons (*c*), thus reaching not only the latter, but also the tip of the radicle (*r*), as can be easily seen in fresh Walnuts which have been immersed for some hours in red ink. In the Cress and Mustard the whole seed-coat takes up water, rendering it slimy and adhesive. A number of seeds, again, have marked corrugations or pittings of the surface of the testa —*e.g.* Corn-cockle (*Agrostemma*), Primrose—in which, after wetting, water is readily retained.

The first result of this absorption of water is invariably the escape of the radicle, and in many plants its penetration into the soil is aided by devices for fixing the seeds (*e.g.* the slimy seed-

coats already mentioned). The culmination of the process of germination is the liberation of the plumule, which is effected in different ways.

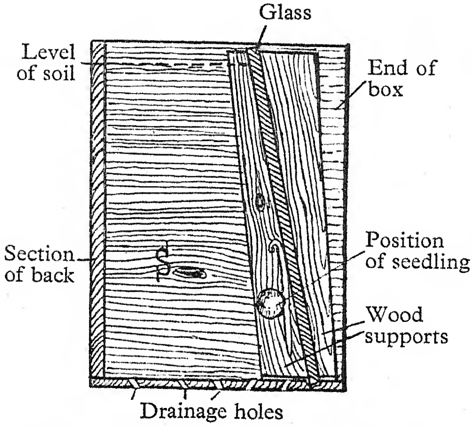

FIG. 20. Diagram of section of box to be used in experiment described on p. 35, showing method of fixing sloping glass front, the position of the seedlings, and the soil (*S*).

In the previous descriptions attention has been drawn to the fact that the young plumule is always protected in some way or other during its passage through the soil, *e.g.* by its own curvature in the Bean, by the coleoptile in the Maize, etc. The straightening of the plumule in the first instance and the bursting through of the enclosed leaves in the second result from exposure to the light on emergence from the soil, and seedlings of either type grown in darkness show no such change. To demonstrate this we can employ a rectangular wooden box which is perforated by a number of small holes to allow of drainage, while one long side is replaced by a sheet of glass sloping inwards from the base at a slight angle (cf. the section in Fig. 20). A thin layer of moist earth is placed on the bottom and seeds are sown in this in close contact with the glass, after which the box is filled with soil. One-half of the glass is covered with black paper, whilst the other remains exposed to the light.

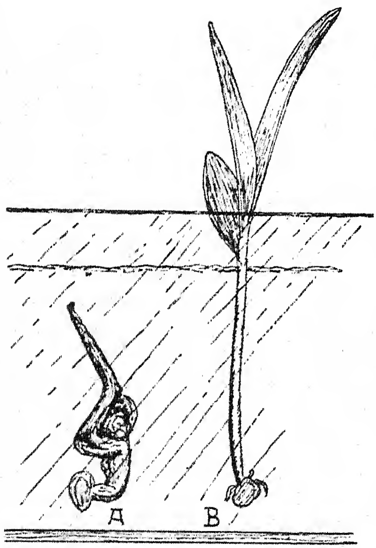

FIG. 21. Two Maize seedlings. A, Grown exposed to light from beginning of germination. B, Grown in darkness till surface of soil is reached. (Reduced to two-thirds natural size.) See text.

The seeds which develop in darkness germinate in the normal way and sooner or

later their plumules appear above the surface (Fig. 21, B). Owing to the inward slope of the glass the plumules remain in contact with it, so that those of the seeds germinating behind the uncovered portion are exposed to the light from the outset, though still beneath the soil. As a result the plumule straightens out or, in the Maize, bursts through the protecting sheath, prematurely. The plumules under these circumstances are so unsuited to force their way through the soil, that they not only fail to reach the surface, but become thrown into folds (Fig. 21, A). This experiment demonstrates that the altered behaviour of the plumule after emergence from the soil is due to illumination, and that without protective devices it would fail to reach the surface. Many herbaceous perennials with underground stems show a similar curvature of the tips of their shoots or of their leaves during their passage through the soil, *e.g.* Dog's Mercury (*Mercurialis*), Moschatel (*Adoxa*), Wood Anemone, etc.

Cotyledons either serve directly as storage-organs or as a means of transference of the food-material from the endosperm. They

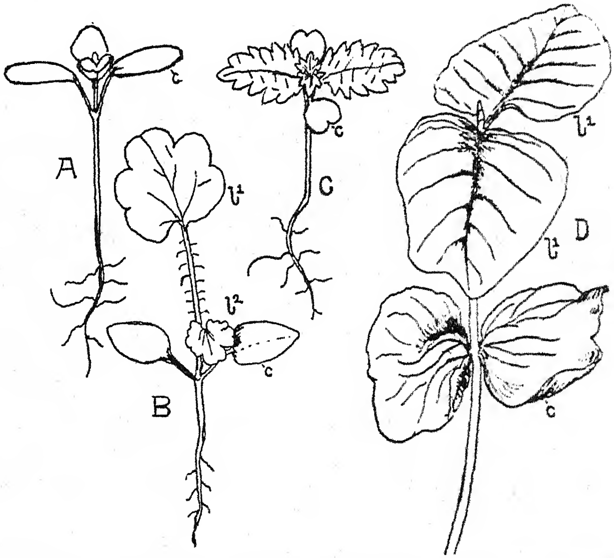

FIG. 22. Different types of Dicotyledonous seedlings (all natural size). A, Garden Spurge (*Euphorbia*). B, Greater Celandine (*Chelidonium*). C, Stinging Nettle (*Urtica*). D, Beech (*Fagus*). *c*, cotyledons; l^1 and l^2, first and second foliage-leaves.

may shrivel after these purposes are fulfilled, or they may subsequently appear above the ground and function for a time as organs

of photosynthesis. Such epigeal cotyledons are always simple in form and among Dicotyledonous plants usually differ to a more or less marked extent from the subsequent foliage-leaves (cf. Fig. 22). Often the leaves following immediately on the cotyledons have a simpler form than those developed later, and this is especially marked in plants whose mature leaves are deeply divided (*e.g.* the Greater Celandine, Fig. 22, B).[1] The foliage may exhibit a progressive increase in complexity as the plant grows older, and a similar transition can often be observed on the shoots of herbaceous perennials, *e.g.* the Musk-mallow (Fig. 23) and the Sheep's Scabious (*Scabiosa columbaria*). Further excellent examples are afforded by young Fern plants (cf. Fig. 254, C, p. 383). Another peculiarity often shown by the first pair of leaves lies in their tendency to arise together from the same node, even when those developed later occur singly (*e.g.* in the Beech, Fig. 22, D, and the Runner Bean, Fig. 12, C.)

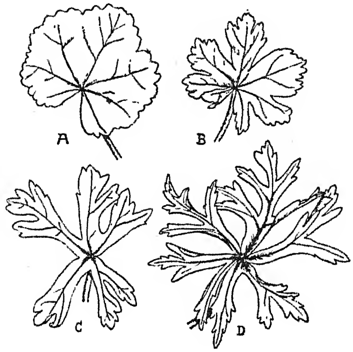

FIG. 23. Transition of foliage in the Musk-mallow (*Malva moschata*) (about half the natural size). A, Radical leaf. B–D, Cauline leaves borne at progressively higher levels on the shoot.

Even in the mature plant the leaves at the base of a branch (prophylls) not infrequently differ from those produced later. Thus, in *Pelargonium* the first two leaves of each branch arise from the same node, whilst the later ones occur singly; in the Willow (*Salix*) the two scales enveloping each bud are the first two leaves of the shoot to which the latter give rise.

[1] For other examples of transition in seedlings, see p. 263 and p. 509.

CHAPTER V

THE STRUCTURE AND PHYSIOLOGY OF THE PLANT-CELL

EVERY living organism, whether animal or plant, is composed of one or more minute *cells*, and this applies even to those forms of life which are so small that they can only be seen with the help of a microscope. The green powdery covering so often present on tree-trunks and palings consists of multitudes of single-celled plants (*Pleurococcus*, Fig. 181, p. 281), whilst millions of cells together form the body of a garden weed or tree. Organisms of the latter type are described as *multicellular*, whilst those consisting of a single cell are termed *unicellular*.

The structure of cells will best be realised if typical examples are studied, such as can be obtained by stripping off the epidermis from the inner surface of an Onion-scale. If a small portion of this be mounted in water, and examined under the low power of a microscope (see Appendix I), it will be seen to consist of a large number of oblong cells connected together without any intervening spaces to form a *tissue* (Fig. 24, A). The network of delicate lines separating the individual units is constituted by the *cell-walls*, which are all joined to one another. In each cell a colourless, somewhat dense granular substance (the *cytoplasm*, Fig. 24, B, *Cy.*) is visible, particularly around the edge, whilst near the centre or against one side is situated a rounded shining body, the *nucleus* (*N*).

These cells consist, then, of three parts, the cell-wall (Fig. 24, B, *C.W.*), which is not living and is merely a protective case, the cytoplasm, and the nucleus; the last two constitute the living part or *protoplast*, composed of protoplasm. The protoplasm [1] is probably a very complex mixture of proteins, fatty bodies, etc., composed mainly of the elements carbon, hydrogen, oxygen, nitrogen, and sulphur (often together with phosphorus, especially in the nucleus). It has somewhat the consistency of the white of an unboiled egg, and usually contains large numbers of small

[1] For details, see W. Seifriz, *Protoplasm.* McGraw Hill Book Co., 1936 (584 pp.).

granules which are partly of the nature of food-bodies and partly waste-products. The fact that not all, though some, of the properties of living protoplasm are exhibited by cells when ground to pulp suggest that the particular characteristics of the cytoplasm are

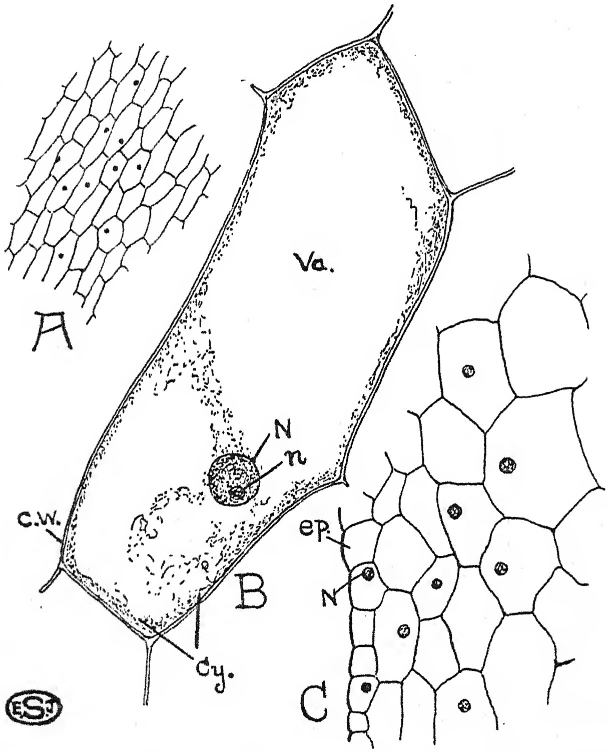

FIG. 24. Epidermis of Onion bulb-scale. A, Small portion in surface view. B, A single cell much enlarged. C, A scale in vertical section. In A and C the nuclei are shown black. *Cy.*, cytoplasm; *C.W.*, cell-wall; *ep.*, epidermis; *N*, nucleus; *n*, nucleolus; *Va.*, vacuole.

not entirely an outcome of its chemical constitution, but are to some extent a consequence of its ultimate structure. The nucleus is a most important part of the protoplast, a fact which will become more apparent when the reproductive processes of plants are studied. It appears to be essential for many of the vital activities of the cell. A demonstration of this is afforded by the fact that, if the unicellular animal *Stentor* is broken into pieces, the fragments which contain portions of the nucleus develop into new individuals, whilst the others, after a short time, perish. Moreover, the nucleus

is generally found in that part of the cell which is in process of active growth, *e.g.* at the tip of a growing root-hair.

The structure of the Onion-cell can be more clearly distinguished if the strip of epidermis be stained with a drop of iodine (see Appendix V), and a single cell examined under the high-power objective. The protoplasm will have assumed a yellowish tint, whilst the nucleus appears pale brown. This colour reaction of the protoplast is one characteristic of proteins generally. The nucleus (Fig. 24, B, *N*) is bounded by a thin *nuclear membrane*, whilst within it one or two small round bodies, the *nucleoli* (*n*), are now plainly visible, since they are stained more deeply than the rest. The cytoplasm does not completely fill the cell, but there is a large space or *vacuole* (*Va.*) occupying the greater part of the central region; this vacuole, apparently empty, is in reality filled with a watery fluid, the *cell-sap*. Close observation shows that the cytoplasm is not evenly granular throughout, but that there is a very thin clear layer immediately within the cell-wall. This layer is perhaps a result of physical forces operating at the surface of the cytoplasm, and a similar clear layer can be detected at the surface abutting on the vacuole. These layers have definite physical properties and are spoken of as the *plasmatic membranes*.

If another strip of Onion epidermis be mounted in concentrated sulphuric acid, the cell-walls will swell and disappear. Subsequent addition of iodine gives a blue colouration to the dissolving walls, a reaction characteristic of *cellulose*, of which most thin cell-membranes largely consist.

It must be realised that the cells just examined, like all plant-cells, are developed in three dimensions, a fact which can be verified by cutting a section transversely across the Onion-scale, when the epidermal cells will appear as flat tabular structures (Fig. 24, C).

As a second example, one of the cells forming the purple hairs (Fig. 25, A) on the stamens of the Common Spiderwort (*Tradescantia*) may be examined.[1] These show the same structure as those of the Onion, but the cell-sap is here of a purple colour. The nucleus, surrounded by a small mass of cytoplasm, is not uncommonly suspended in the middle of the vacuole, the enveloping cytoplasm being connected with that lining the cell-wall by a number of protoplasmic strands (Fig. 25, B). If the granules in these strands are closely observed, they will be seen to exhibit a continuous streaming movement which can be accelerated by *slight*

[1] If material of the Spiderwort is not available, a good substitute is furnished by the unicellular hairs lining the inner surface of the corolla-tube of the White Dead-nettle, in which, however, the cell-sap is uncoloured.

warming, but ceases on the addition of a poison (*e.g.* alcohol), whereby the cell is killed. A temporary cessation of the movement can be brought about by mounting the cells in water to which a trace of some anæsthetic (*e.g.* chloroform) has been added. On returning the hairs to ordinary water, however, streaming of the granules is soon resumed. Energy provided by respiration is necessary for such movements. If the cells are mounted in water which has been boiled and subsequently cooled, the cessation of movement shows the necessity of oxygen. The movement is really due to a flowing of the cytoplasm, and this phenomenon betrays the fluid consistency of the latter. No movement can be recognised, however, in the plasmatic membranes, which are therefore probably of a denser character.

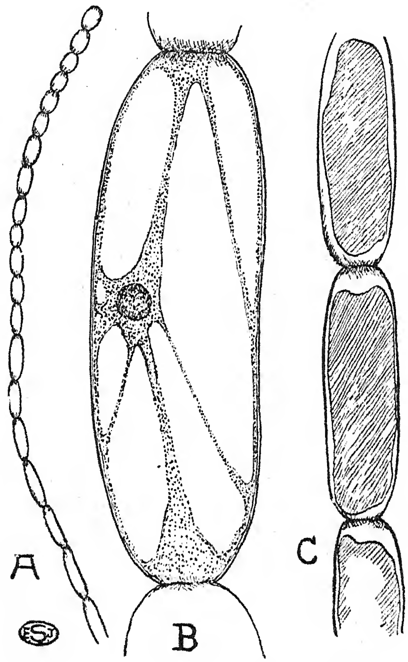

FIG. 25. Staminal hairs of the Spiderwort (*Tradescantia*). A, a single hair; B, a single cell showing the nucleus and strands of cytoplasm passing across the vacuole; C, a hair plasmolysed with sea-water.

All living plant-cells display the features above described, but in many, other structures are present, of which the commonest are bodies known as *plastids*. In those cells of the plant which are exposed to the light the plastids become the depositories of the *chlorophyll*, and are then known as *chloroplasts*. On examining a leaf of the Canadian Pondweed (*Elodea canadensis*) under the high power, each of the more or less rectangular cells will be found to contain a number of chloroplasts, which will be seen from one of two aspects (Fig. 26). Some, situated along the sides of the cell, are viewed in profile and appear as flattened ellipses (*O.S.*), whilst others lying against the upper or lower walls, and consequently seen from the surface, present a round or oval form (*Su.*). Each chloroplast is thus a solid body which has more or less the shape of a biconvex lens.

If attention be centred on a single cell, the chloroplasts lying

against the upper face can be brought clearly into view by turning the fine adjustment; on focussing to a lower level, however, another layer of chloroplasts appears belonging to the same cell. Each cell can thus be likened to an oblong box lined along the whole of the inner surface with a thick viscid fluid (the cytoplasm) in which are embedded the chloroplasts, the cavity of the box representing the vacuole (Fig. 26, *Va.*) with its cell-sap.

By watching the chloroplasts, particularly in the elongated cells of the midrib, they will be observed to exhibit movement similar to that of the granules in the cells of the Spiderwort, and here as there this is actually due to a flow of the cytoplasm. Such a streaming movement probably takes place in the cytoplasm of all living cells, but in many it is so slow that it cannot be demonstrated. By its means food-substances, etc., are more quickly distributed from one part of the cell to the other than by mere diffusion.

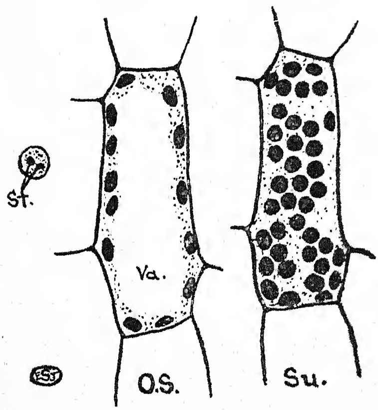

FIG. 26. Two cells of the Canadian Pondweed, one in surface view (*Su.*), and the other in optical section (*O.S.*). The chloroplasts are shown black. At the left a single chloroplast showing starch grains (*St.*). *Va.*, vacuole.

When leaves of the Canadian Pondweed, or those of other plants, are kept in spirit for some little time, all the chlorophyll is removed in solution. The chloroplasts, though now colourless, have undergone no change of shape, and are therefore merely specialised parts of the cytoplasm which hold the chlorophyll.

The green cells of all the higher plants contain numerous chloroplasts, essentially similar in form to those just studied. In the Algæ (p. 295), however, the cells are often provided with but a single chloroplast or a limited number of them, and these are frequently of a much more elaborate pattern. *Spirogyra*, which is exceedingly common in stagnant water, furnishes an extreme instance. The plant here consists of a single thread or filament composed of cylindrical cells joined end to end. According to the species, each cell contains, apart from the cytoplasm and nucleus, one or more chloroplasts in the shape of green spiral bands, usually with a jagged edge (Fig. 27, *ch.*). These spiral chloroplasts are here, again, situated in the lining layer of cytoplasm. At intervals

bright bodies, consisting of protein and known as *pyrenoids*, are embedded within their substance (Fig. 27, *p.*); but these are more evident after treatment with iodine, whereupon they become blue, owing to the fact that each is surrounded by a layer of starch. Pyrenoids are not found in the chloroplasts of the higher plants, but are quite frequent amongst the Algæ (see p. 295).

Returning to the cells in the hairs of the Spiderwort, we will mount them in 2 per cent. natural or artificial sea-water (see Appendix VI); the resulting phenomena could be equally well observed by using any cells with coloured sap, *e.g.* those forming the lower epidermis of the Mother-of-Thousands (*Saxifraga sarmentosa*), or of the Cyclamen. In the cells thus treated the lining layer of cytoplasm has contracted away from the wall, so that a clear region occupied by sea-water is visible between it and the wall (Fig. 25, C). In this condition the cell is said to be *plasmolysed*, and the phenomenon is spoken of as *plasmolysis*. If the sea-water be replaced by tap-water, the cell-sap increases in volume, so that the plasmatic membrane regains its original position, pressed up against the wall, and the cell resumes its normal appearance. By alternately substituting sea-water and tap-water, this sequence of events may be repeatedly observed.

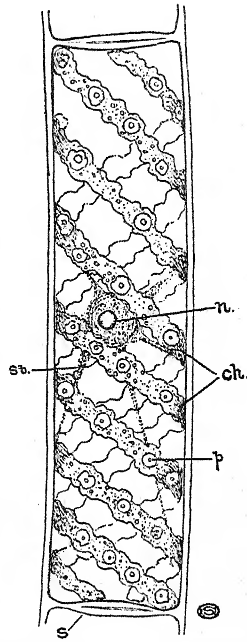

FIG. 27. Single cell of a *Spirogyra*-filament showing the spiral chloroplast (*ch.*), the pyrenoids (*p.*) surrounded by starch, and the nucleus (*n.*) supported by cytoplasmic strands (*st.*). *S*, separating wall between adjacent cells.

In the normal cell the pressure of the sap within the vacuole keeps the lining layer of cytoplasm distended and forced against the wall, in much the same way as the bladder of a football, when inflated with air, is pressed against the leather cover. If the air be allowed to escape, the bladder shrinks and a space is left between it and the cover. Similarly, the contraction of the protoplast of the cell, when surrounded by sea-water, must be attributed to a decrease in volume of the cell-sap owing to passage of water into the outside liquid. The recovery, when placed in water, obviously implies an increase in volume of the sap, and this can only be due to some of the water around having passed into it.

It is a well-known physical phenomenon (*osmosis*) that, when two

solutions of different concentrations are separated by a membrane (which may be of a fluid consistency) that is permeable to the solvent (*e.g.* water) but relatively impermeable to the substances in solution, a passage of water tends to take place through the membrane from the weaker solution to the stronger. Membranes possessing this property are said to be *semi-permeable* with respect to the substance in solution. This attribute thus depends both upon the nature of the membrane itself and upon the solution in relation to which it is used.

To demonstrate osmosis it is most convenient to use the semi-permeable membrane afforded by the membranous precipitate of copper ferrocyanide which is formed when solutions of copper sulphate and potassium ferrocyanide meet. This membrane is itself too weak to withstand pressure and is most suitably deposited in a supporting membrane of celloidin (see Appendix VII) fitted over the open end of a thistle funnel. The solution whose osmotic pressure is to be investigated is placed in such an osmometer, and the whole is immersed in pure water so that diffusion between the two solutions can only take place by way of the semi-permeable membrane. The osmotic pressure of the solution can then be calculated from the height to which it rises within a glass tube fitted on to the osmometer, or by means of a suitable manometer.

The lining layer of protoplasm, or probably more correctly the plasmatic membranes, exhibit a varying degree of semi-permeability. Consequently, when cells are surrounded by solutions of substances to which the plasmatic membrane is relatively impermeable and which are more concentrated than the cell-sap, water passes out and the protoplast contracts. On the other hand, when replaced in water, the cell-sap is the more concentrated solution, and the protoplast becomes distended until its further expansion, and further increase in the volume of the sap, is limited by the stretching capacity of the cell-wall. In a healthy plant, supplied with sufficient water, all the living cells are thus distended, that is to say they are *turgid*, a condition which plays an important part in maintaining the stability of herbaceous organs (see p. 143). Absorption of water by the cell also depends to a varying extent upon imbibition (p. 50) by colloidal substances in the protoplast or cell-sap.

If cells were completely permeable, the concentrations inside and outside would rapidly become equal as a result of diffusion, and plasmolysis could not occur, nor would turgidity be possible. Cells are, however, relatively impermeable to many substances in solution, although when living cells are left immersed in a plasmolysing solution, the gradual recovery from plasmolysis which is often observed, after a longer or shorter interval, shows that slow inward

diffusion of the solute may occur (*endosmosis*). In some plants this is an important means of adjustment to changes of concentration in the soil-solution (cf. p. 566).

The plasmatic membranes exhibit their semi-permeable character, however, only so long as the protoplast remains alive; hence after death both the substances dissolved in the cell-sap can pass outwards, and external solutions can diffuse inwards. If cells of the Spiderwort, etc., mounted in water, are killed by gently heating the slide over a spirit-lamp, the coloured sap will be found to escape into the surrounding liquid; moreover, it will be found impossible to bring about plasmolysis or to render such killed cells turgid. These results, apart from showing that the semi-permeable character of the cytoplasm is altered by death, demonstrate that the cell-wall is readily permeable to substances in solution. The permeability of the cytoplasm, when dead, to the cell-sap may be exhibited on a large scale by placing slices of Beetroot in hot water.

A moment's thought, quite apart from any experimental demonstration, shows that the plasmatic membranes must be permeable to many substances, since most of those dissolved in the soil-water can be detected within the plant. Moreover, plants will thrive for months or years in a solution of mineral salts from which analysis shows that the latter have been absorbed (cf. p. 206).

Were it not for the restraining influence of the wall, which is only slightly extensible, but possesses considerable strength, a plant-cell placed in pure water would increase in size until it became ruptured. This actually occurs when the root-hairs of salt-marsh plants are suddenly transferred to water, for these have a highly concentrated sap. The more concentrated the sap, the more strongly does it absorb water, and the greater will be the pressure upon the wall exerted by the protoplast as it swells. The maximum force with which a solution tends to take up pure water through a semi-permeable membrane is called the *osmotic pressure* of the solution.

The cell-sap has a variable osmotic concentration of molecules and ions which confers upon it a potential capacity to absorb pure water, when separated from it by a semi-permeable membrane. When water is absorbed, the consequent swelling of the cell-contents causes an outwardly directed pressure (*turgor pressure*) to be exerted on the wall, which stretches the latter until the increasing pressure of the stretched wall (*wall pressure*) becomes great enough to resist any further increase in the volume of the cell-contents. So long as this limit is not reached, an isolated cell has a power to absorb water (*suction force* of the cell), which is equivalent to the difference between the force due to the osmotic concentration of the sap and the wall pressure. It is upon differences in suction

force that exchange of water between adjacent living cells depends. At any time the intake of water by a cell of a tissue [1] depends on the difference between its absorbing force due to osmotic concentration and the forces tending to remove water from the cell, viz. (*a*) the pressure of the wall and that of the surrounding cells which oppose any increase in volume, and (*b*) the suction force exerted by the *other* living cells around, which are also competing for water.

Loss of water from cells, as in transpiration, or gain in water, as in absorption by root-hairs, lead to alterations in the suction force of the cells concerned, and therefore establish gradients in suction force between these and neighbouring cells, by virtue of which movement of water from cell to cell and from one part of the plant to another takes place (cf. p. 193).

By using artificially prepared semi-permeable membranes (see Appendix VII) the osmotic pressure of a solution can be determined in terms of atmospheric pressure. In general the osmotic strength of a solution depends upon the number of molecules it contains, though this does not apply to dilute solutions of electrolytes in which the osmotic pressure is increased by dissociation of the ions. When the molecules are present in equal proportions, two solutions of cane-sugar and grape-sugar, for example, have the same osmotic pressure. Such *equimolecular* solutions are obtained by dissolving substances, in a litre of distilled water, in proportions equivalent to their molecular weights. If the number of grammes of the compound dissolved in a litre of water is equal to the molecular weight, we have a so-called gram-molecular solution, briefly indicated by *M*. Solutions of other strengths are indicated as 0·5 *M*, 0·2 *M*, etc. Since the weight of a substance depends on the number and mass of the atoms composing its molecule, a 10 per cent. solution of a complex compound, such as inulin or dextrin, will contain fewer molecules than a 10 per cent. solution of a simpler compound, such as grape-sugar or cane-sugar; moreover, cane-sugar, which has a higher molecular weight than grape-sugar, will exhibit a lower osmotic pressure than the latter when in solutions of the same *percentage* strength. These important facts are illustrated in the following table:

	Molecular weight.	Molar concentration of 10 per cent. solution.	Osmotic pressure in atmospheres.
Grape-sugar .	180	0·555	12·43
Cane-sugar .	342	0·292	6·54
Dextrin . .	—	—	ca. 2·2
Albumen	ca. 13,000	0·008	0·17

[1] Even when a cell forms one of a tissue, it can receive water from all sides as long as the water-supply is normal, since all parts of a healthy plant imbibe water (cf. p. 59).

In order to estimate the osmotic pressure within a cell, a solution of sea-water (see Appendix VI), strong enough to bring about plasmolysis, is first obtained. By experimenting with a series of solutions of diminishing strengths, one can eventually be found which just fails to cause plasmolysis, and which is slightly weaker than another which brings about a very slight, but often local, contraction of the protoplast from the wall. The former solution gives the approximate osmotic concentration of the sap at the moment of plasmolysis (for equivalent pressures, see Appendix VI). The value determined is somewhat higher than the osmotic concentration of the sap of the normal cell, owing to the contraction of the stretched wall as the turgor-pressure diminishes and because water has been withdrawn during the experiment. It will, moreover, not be a true value unless the membranes can be assumed to be completely semi-permeable. More accurate determinations of the osmotic pressure of the cell-sap are made by indirect means, depending on the relation between osmotic pressure and the temperature at which a liquid (*e.g.* the expressed sap of a plant-organ) freezes.

In one and the same plant the osmotic concentration of the sap shows diurnal fluctuations and varies (sometimes as much as ten atmospheres in a day) with the humidity of the environment.[1] Very low values are characteristic of water-plants, whilst the highest osmotic concentration recorded is that of a desert plant, *Atriplex confertifolia*, in which 153 atmospheres may be realised.

The average suction force of the cells of a tissue is readily determined by the following method, depending upon the curvatures consequent upon the different stretching capacities of the walls of the component cells. Short lengths of the stalk of a Dandelion-inflorescence, split lengthwise into four portions, are placed in water. Since the cells towards the outside of the stem have thicker walls than the inner ones, the latter have a greater aggregate stretching capacity and the strips curl up and form rings. A strength of sea-water that causes neither increase nor decrease in the curvature will give an approximate measure of the average suction force of the cells. Stems of many herbaceous plants can be utilised in this way.

The protoplast is very readily permeable to a number of organic substances, and these can be used to investigate this phenomenon. Thus, if young shoots of the Canadian Pondweed be placed in a solution of methylene blue, so weak that it has but a very faint tint, the cell-contents will after some days be found to have assumed a deep blue colour. This indicates that the dissolved dye has

[1] In *Helleborus fœtidus* osmotic pressures ranging from 10·5 to 66 atmospheres have been observed.

passed through the cytoplasm in considerable amount. If the methylene blue remained unaltered on reaching the vacuole, only sufficient could have entered to bring about a concentration equivalent to that of the solution outside the cells. But the deep blue colour shows that the dye has accumulated within the sap, and this is due to the combination of the methylene blue with the tannin in the latter to form a substance to which the plasmatic membrane is impermeable. In this way the concentration of the dye which enters the cell-sap is continually being reduced to a strength below that outside. As a consequence more and more methylene blue diffuses in, and thus the deep blue colour is gradually produced.

A further demonstration of permeability of the cytoplasm is obtained when filaments of *Spirogyra* (and many other Algæ) are placed in a dilute (1 per cent.) solution of caffeine. Under the microscope there is seen to appear in the vacuole a very fine greyish precipitate which, as it accumulates, renders the cell more and more opaque. This precipitate is again a consequence of combination between the tannin in the cell-sap and the caffeine.

Both examples illustrate the very important phenomenon that plant-cells can absorb *and accumulate* considerable quantities of various substances *from very dilute solutions* by diffusion, provided that within the cell they are changed into some other form which is insoluble or does not readily pass through the plasmatic membrane, or that they are adsorbed (see p. 50) by colloidal substances. This fact is significant when it is remembered that many compounds are only present in the soil-water in very small amounts. The phenomena just discussed also explain the accumulation of food-reserves (*e.g.* starch) in large quantities in the cells of storage-organs. When these reserves are utilised, it is clear that they must be changed into a form which can diffuse to the growing organs, insoluble starch, for example, being transformed into soluble sugar. This process can be simulated by placing leaves of the Canadian Pondweed, whose cell-sap has acquired a deep blue colour in the way above described, in a very dilute solution of citric acid (1 per cent.). The latter passes into the cells and changes the blue pigment into a form capable of diffusing through the plasmatic membrane. Since its concentration inside the cell is greatly in excess of that outside, diffusion takes place and the sap gradually loses its deep blue colouration.

Mineral salts, when used singly and in a sufficiently concentrated solution, may bring about contraction of the protoplast of plant-cells (*e.g.* root-hairs). Osterhout has shown that many, and perhaps all, of these instances of so-called plasmolysis are due, not to impermeability of the plasmatic membrane to the substance in question,

but to a poisonous or toxic effect of the latter upon the protoplasm. Two substances, however, which separately exert such a harmful effect can often, if mingled in appropriate proportions, provide a solution which produces no plasmolysis and is not poisonous. In the relatively dilute solutions of these compounds that are employed dissociation of the molecules into ions takes place, and the results just described are probably due to an effect of the metallic ions upon the proteins of the plasmatic membrane.

The prevention of the poisonous action of one ion by one or more other ions is spoken of as *antagonism*, and is probably greatest between ions of different valencies. A mixture of ions in solution in such proportions that they exert no toxic effect is called a *balanced solution*, and when a solution of this nature produces contraction of the protoplast, the effect is a true plasmolysis. In this category may be placed sea-water, which is a mixture consisting mainly of sodium chloride, magnesium chloride, magnesium sulphate, potassium chloride, and calcium chloride, and for this reason sea-water suitably diluted forms the best medium for determining osmotic pressures in the plant-cell.

It will be realised that the rate of entry into a cell of one ion, whether toxic or not, may be markedly influenced by the presence of other ions. The complexity of the phenomena of diffusion is illustrated by the fact that roots do not absorb compounds in the same proportions as they occur naturally in the soil-solution (p. 208) and that the intake of water and of dissolved salts are both influenced by the rate of respiration.

Of the diverse compounds found within the cells of plants, and continually being transported from one organ to another, some diffuse readily through membranes (*crystalloids*, *e.g.* mineral salts and sugars), while others are indiffusible (*colloids*, *e.g.* gums and proteins). The difference between the two as regards diffusibility is so marked that mixtures of crystalloids and colloids in solution are readily separated by dialysis, *i.e.* by placing the solution in a parchment tray floating on a large volume of water. In general, crystalloids, in contradistinction to colloids, are substances which readily crystallise and which form true solutions. Under certain circumstances, however, many, and perhaps all, crystalloids can be caused to show colloidal features. It is thus more correct to speak of the colloidal state, in which many substances naturally occur.

Colloids can, by certain and varied treatment, be caused to form so-called solutions which, however, differ from true solutions in being non-diffusible and in other respects. Such a *sol* is obtained, for instance, when boiling water is added to starch paste

(p. 75). In all true solutions the molecules or ions of the solute may be assumed to exist independently in the solvent. In a sol, however, the molecules are probably aggregated in small groups, which remain permanently suspended owing to electrical forces. In sols like those of the metals the suspended particles are solid, and such sols grade imperceptibly into suspensions, such as that obtained when clay is shaken up with water. Other sols, however, contain liquid particles in suspension and are, therefore, of the nature of emulsions (*e.g.* oil in water, milk, latex, see p. 96). At the other extreme colloidal solutions grade over into true solutions.

Sols are distinguished from ordinary suspensions and emulsions by the finely divided state of the particles. These latter can only be detected with the ultra-microscope, and only when relatively coarse; they are then seen to exhibit a constant oscillation due to surface action (*Brownian movement*). By various means (change of temperature, addition of electrolytes, shaking, etc.) the suspended particles of a sol are caused either to precipitate, or the whole sol sets to form a jelly-like mass, or *gel*. This latter is seen in the setting of solutions of gelatine or agar-agar, when cooled, or the coagulation of proteins (*e.g.* white of egg), when heated. Sometimes, though by no means always, these changes are reversible. The solid particles of a gel probably form a continuous phase, in the numerous interstices of which the liquid is held. Living protoplasm may have the structure of a gel and, like the latter, possesses the important property of imbibing water with which it is usually saturated. This property of gels no doubt depends on their large internal surface, although the amount of imbibition is greatly influenced by the acid or alkaline reaction of the imbibing substance.

The individual molecules comprising the particles of a colloidal solution exert an attraction upon one another, but it will be obvious that, at the surface of each molecular aggregate, there is an unsatisfied molecular attraction which, though very limited in its sphere of action, is, within that sphere, very powerful. Consequently molecules of foreign substances, which come within its domain, may become attached to the surface of the molecular aggregates. Such *adsorption* is very pronounced in gels which usually have the capacity to take substances out of solution and to retain them very energetically. It is possible that, on the large surface afforded by the colloidal complex of the protoplasm, many chemical reactions may take place between the adsorbed substances.

CHAPTER VI

MERISTEMS AND CELL-DIVISION

IN some of the simpler forms of plants (*e.g. Spirogyra*) almost every cell may exhibit growth and division, but, in the vast majority, the cells originate in the first instance by division from meristems (growing points) (p. 6), usually situated in a Flowering Plant at the tips of the stem and root and of their respective branches. A similar apical position of the meristem commonly obtains amongst the lower plants.

A good example is afforded by the Seaweed *Sphacelaria*, which is found in rock-pools. Here each branch ends in a single large cell (Fig. 28, *a*). During the active season of the year this cell is constantly increasing in size, and, when it has attained a certain length, it becomes halved by the formation of a cross-wall (Fig. 28, *b*). The upper portion again enlarges until a new septum arises, whilst the lower half (termed a segment) undergoes further division (Fig. 28, *c–e*) to form the cells of the mature plant. The Seaweed *Dictyota* furnishes another good instance of a unicellular growing point, whose mode of division will be understood by reference to Fig. 29. The daughter-cells or segments in these two Seaweeds are cut off in a single series parallel to one face of the cell.

In most plants having a unicellular meristem the apical cell has the form of a three-sided pyramid with a rounded base directed outwards (Fig. 30, *a.c.*); such a cell is described as *tetrahedral*. Segments are here cut off in succession from each of the three flat inner faces, these segments undergoing further subdivision to form the mature tissues. This type is found in Mosses and Ferns, and can be readily examined in a longitudinal section through the tip of the stem of a Horsetail Fern (*Equisetum*) (Fig. 30). In such a section the apical cell (*a.c.*) of course appears triangular, and two only of the three series of segments are visible. In the roots of Horsetails and Ferns which possess such a unicellular meristem its mode of division is similar, but segments are also cut off parallel to the rounded base, the cells produced by their subdivision forming the root-cap.

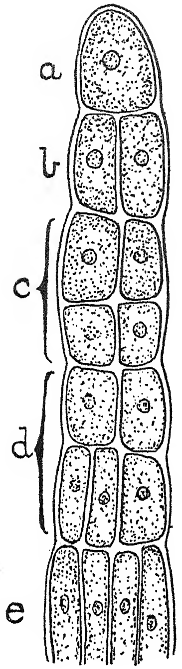

FIG. 28. End of a branch of *Sphacelaria.* The successive segments cut off from the apical cell (*a*) are lettered in order from the youngest to the oldest (*b–e*), and show increasing subdivision.

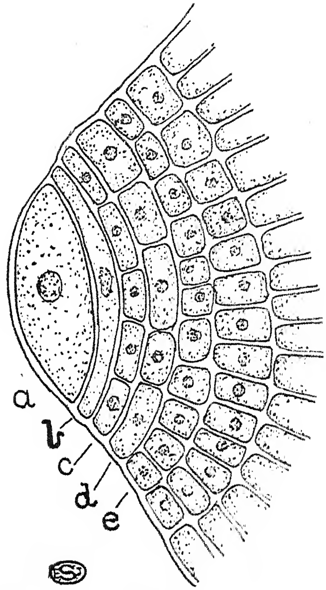

FIG. 29. Growing point (*a*) and adjacent part of the thallus of *Dictyota.* Lettering as in Fig. 28.

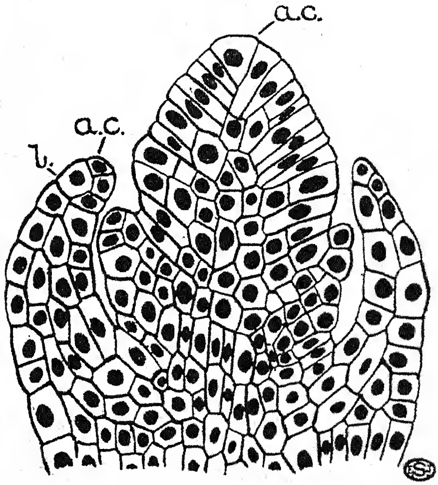

FIG. 30. Growing apex of the Giant Horsetail (*Equisetum maximum*) in longitudinal section, showing the tetrahedral apical cells of the stem and leaf (*a.c.*); *l*, leaf.

The growing region of the higher plants consists of a tissue of small actively enlarging and dividing elements, which takes the place of the single cell of the lower plants. Such a *meristem* is best examined by cutting longitudinal sections through the apex of stem or root. In both organs the cells of the meristem are arranged in several layers (Fig. 31) which can be traced back into the different regions of the mature plant. As the meristematic cells multiply, those that remain near the apex retain their power of

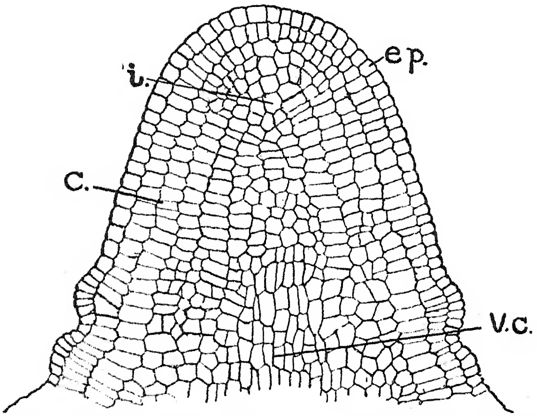

FIG. 31. Meristem of the stem of the Mare's Tail (*Hippuris*) in longitudinal section, showing the regions of vascular cylinder (*V.C.*), cortex (*C.*), and epidermis (*ep.*), and the single meristematic cell (*i.*) from which the vascular cylinder arises.

division, whilst those that come to lie farther back gradually pass over into permanent tissue.

In the stem the outermost layer of the meristem usually divides only by walls at right angles to the surface to produce a single layer (*dermatogen*) which, in the mature region, can be recognised as the *epidermis* (Fig. 31, *ep.*). The innermost cells divide in all directions, and can be traced back into the central region of the stem, which latter consists of the *vascular strands* and pith (*V.C.*). The middle layers of the meristem also segment in like manner, and develop into the tissue situated between the epidermis and the vascular strands, a part of the mature stem known as the *cortex* (Fig. 31, *C.*). In some plants three meristematic regions are distinguishable, known as the *dermatogen*, *periblem*, and *plerome*, which respectively give rise to the epidermis, cortex, and vascular cylinder of the adult.

At the growing apex of the root four meristematic layers are often distinguishable. Three, the dermatogen, periblem, and

plerome, serve the same purpose as in the stem; but external to the dermatogen is a fourth layer, the *calyptrogen*, which cuts off segments towards the outside only, and thus gives rise to the root-cap (Fig. 32). The latter is constantly replenished by the meristem, as the older cells in front become disorganised. In

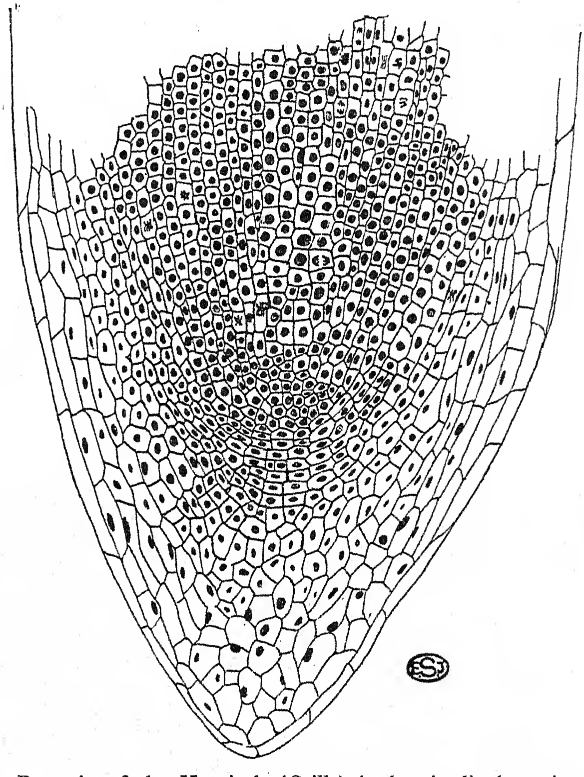

FIG. 32. Root-tip of the Hyacinth (*Scilla*) in longitudinal section showing the meristem and the root-cap. Some of the nuclei (black) exhibit phases in nuclear division.

many roots, however, the epidermis and root-cap arise from a common meristematic layer, and other modifications are also found.

At the base of the internode in Grasses, and at the top of the internode in Labiatæ, occur intercalary meristems, which consist of a transverse plate of small meristematic cells in which no definite regions can be distinguished.

In the process of *cell-division* [1] the nucleus always takes the lead,

[1] For details, see C. D. Darlington, *Recent Advances in Plant Cytology*, J. & A. Churchill, 1932 (559 pp.); and L. W. Sharp, *Introduction to Cytology*, 3rd edit., McGraw Hill Book Co., 1934 (567 pp.).

dividing into two parts, or daughter-nuclei, which become separated from one another by the development of an intervening wall. Thus two new cells are established, each with its own nucleus, similar in all respects to that of the cell from which they originated. Amongst some of the lower plants, and as a rare phenomenon in the higher, the nucleus merely divides into two portions by a median constriction. This is spoken of as direct nuclear division (*amitosis*).

More usually, however, there is a sequence of complex changes in the nucleus preparatory to and during division, and this whole process is designated *mitosis* or indirect nuclear division.[1] All stages can be seen in a thin longitudinal section through the meristem of a higher plant (cf. Fig. 32); but in order to observe them readily, it is necessary to employ material which has been carefully preserved and suitably stained (see Appendix IV).

The nucleus is ovoid or spheroidal in form (Fig. 24, B, *N*; 34), and, when not actually dividing, is spoken of as the *resting or vegetative nucleus*; the former term, however, is apt to be misleading, since in this state the nucleus is probably just as active. Within the nuclear membrane (p. 40) there are granules of deeply staining substance (*chromatin*) which often appear to be connected by fine strands to form a more or less irregular network (Fig. 34, A). There are also within the nucleus one or more larger nucleoli, which likewise stain deeply. The rest of the nucleus is occupied by the *nuclear sap*, which does not take up stains.

The early stages of nuclear division (*prophase*) are characterised by the appearance of thin paired beaded strands (Fig. 33, A) in which the beads, probably representing the granules seen in the resting nucleus, are known as *chromomeres*. Gradually the threads become thicker and stain more deeply, and simultaneously the beaded appearance may no longer be recognisable. At this phase the nucleoli generally disappear. The thickened paired threads are termed *chromosomes* (B) and each part a chromatid; in some plant nuclei which have been studied in detail, each pair has a characteristic form. The number of chromosomes is usually constant for the vegetative cells of any particular species.

As the chromosomes become recognisable the nuclear membrane disappears and the region of the nucleus is seen to be occupied by a denser body of protoplasm shaped like two cones with their bases in contact (Fig. 35, A). Perhaps as a result of loss of water during fixation, this double cone exhibits striations from the two apices or poles towards the common base or equatorial plane; this structure constitutes what is known as the *nuclear spindle*. In

[1] The term *karyokinesis* is now rarely employed.

some way each chromosome becomes attached at a definite point along its length to the equator of the spindle, the free portions of the chromosomes occupying various positions in the cytoplasm (Fig. 35, B and C). This stage constitutes the *metaphase*.

The succeeding stage, known as the *anaphase* (Fig. 33, D), is

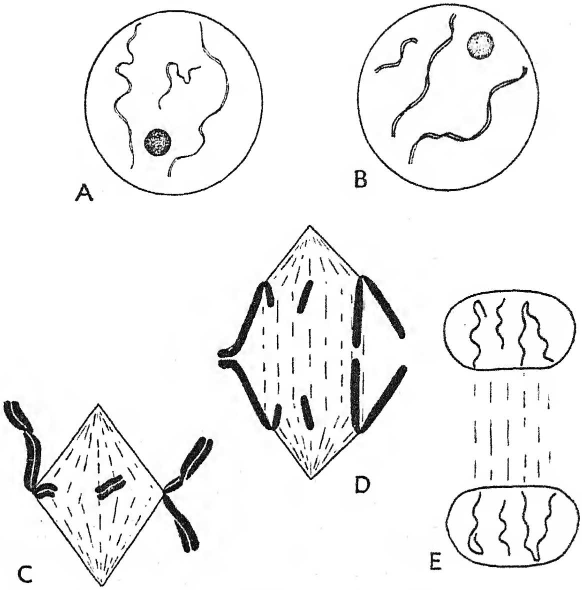

FIG. 33. Diagram to illustrate mitosis. For the sake of simplicity a haploid nucleus containing three chromosomes is represented. [The normal vegetative nucleus of higher plants is diploid and contains each kind of chromosome in duplicate.] A, Early prophase; each chromosome appears as a double thread. B, Late prophase; in each chromosome the sister chromatids are now thicker, the nucleolus is becoming less chromatic. C, Metaphase; the chromosomes are attached at the equator of the spindle by their constrictions. D, Anaphase; sister chromosomes (the chromatids of the prophase) passing to the poles. E, Telophase; a nuclear membrane has appeared round each daughter-nucleus in which the chromosomes are becoming decreasingly chromatic (one or more nucleoli will appear in each nucleus).

characterised by the passage of the respective halves (chromatids) of each chromosome to the opposite poles of the spindle. The movement is accompanied by an elongation of the middle region of the spindle, which thus becomes cylindrical. The attached region of each chromosome is directed forwards, as it moves towards the pole, and the form of the chromosome is associated with this; when the attachment is terminal the chromosomes are usually rod-shaped, when the attachment is subterminal they appear J-shaped, whilst when median the chromosomes tend to be V-shaped. These forms

suggest that there are forces drawing apart the two halves of a chromosome.

From the separation of equivalent halves of the original chromosomes of the parent nucleus to opposite poles (Fig. 35, D), there result two groups around each of which is formed a nuclear membrane. The chromosomes in each daughter-nucleus now stain less readily and lose their visual distinctness, whilst one or more nucleoli

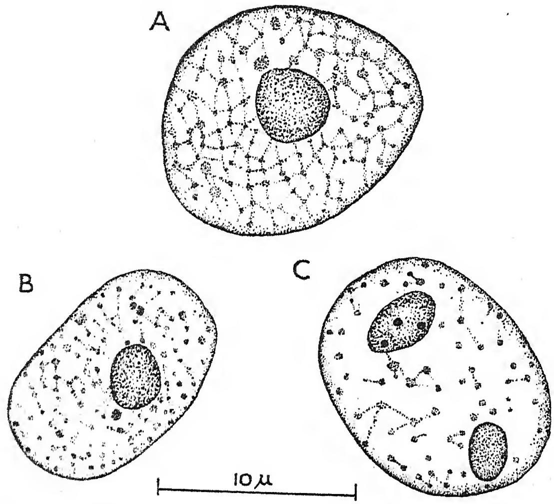

FIG. 34. "Resting" nuclei from fixed and stained preparations of A, *Alstrœmeria aurantiaca*; B, *Bomarea multiflora*; C, *Hypoxis Rooperi.*

appear. This stage, which is roughly the reverse of the changes occurring during prophase, is known as *telophase* and leads to the formation of two resting nuclei, each with the same number of chromosomes as the parent nucleus. As this process is repeated at every division, all the vegetative cells [1] of the plant come to possess nuclei with the same number of chromosomes.

As the daughter-nuclei are reconstituted, thickenings appear in the equatorial plane, probably due to a modification of the cytoplasm in this region. These thickenings become more conspicuous as they extend horizontally across the parent-cell, till finally they join to form a complete diaphragm of modified cytoplasm, the *cell-plate*. Within the latter there is formed a thin membrane of calcium pectate which separates the two daughter-cells, and is traversed by fine cytoplasmic connections. These persist, so that protoplasmic connections are present between adjacent

[1] For details of nuclear division in reproductive cells, see p. 590.

cells of the adult plant. Subsequently further layers, consisting largely of cellulose, are deposited on either side of the original membrane (see next chapter), which is the only part of this separating wall common to the two daughter-cells. These

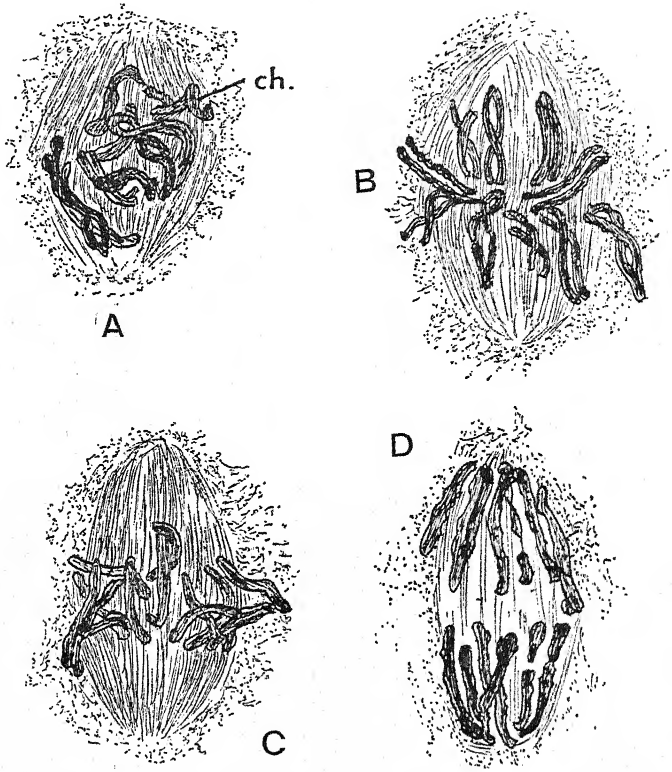

FIG. 35. Some stages in mitosis of *Vicia faba* (after Fraser and Snell). A, Establishment of spindle; *ch*, chromosome. B, Metaphase. C, Chromosomes at equator of spindle. D, Chromosomes have separated and reached the poles.

additional layers frequently become chemically changed in various ways, but the original separating wall, termed the *middle lamella* (Figs. 37, 38, *m.l.*), does not usually undergo such profound modification, so that it is readily distinguished by its different density, and often stains more deeply.[1]

From the foregoing it is evident that, when cell-division takes place, the nuclei of the daughter-cells are derived from that of the

[1] The separating wall in many Algæ arises as an ingrowing diaphragm (Fig. 183, E, p. 285), and is not always directly related to nuclear division.

parent-cell. This fact holds generally throughout the Vegetable and Animal Kingdoms, the nucleus of any given cell always being the product of a pre-existing one. The origin of a new nucleus from the cytoplasm is unknown. In like manner it is probable that chloroplasts (and other plastids) multiply by division and are derived from pre-existing specialised cytoplasmic bodies. During the enlargement usually following upon cell-division considerable increase of the cytoplasm may take place; but it should be emphasised that new protoplasm is only formed in connection with a pre-existing protoplast, the independent origin of living matter being unknown. In other words, both in the Animal and Vegetable Kingdoms, one generation is merely a continuation of the previous one, the reproductive cells of any one dividing and enlarging to form the body of the next.

We can now consider how the cells produced at the meristem gradually pass over into the mature condition. Just below the apex they have dense cytoplasmic contents, are more or less rectangular or polygonal, and fit closely together, without any interspaces. A little farther back, representing an older phase, they increase appreciably in size and often become more or less rounded off, as a result of which small spaces, the *intercellular spaces* (Fig. 56, *i.p.*), appear between them, particularly at the angles. Where increase in size involves considerable elongation, the cells may slide by one another, resulting in what is called *gliding growth.*

The increase in volume of the cells is almost entirely due to the intake of water which results from the formation of substances that bring about an increase in osmotic pressure. These substances are produced during the living processes carried on in the cells, and, as a consequence of their solution, a number of small vacuoles containing cell-sap appear in the cytoplasm (vacuolisation). These vacuoles gradually increase in size, and ultimately coalesce to form one (*e.g.* Onion, Fig. 24) or few large vacuoles. Apart from its presence in the vacuoles, however, water also permeates the protoplasm and cell-wall, forming the so-called *imbibition-water*.

With the gradual assumption of the mature condition the cells generally lose their power of division, though this faculty may be again stimulated into activity, as when a plant is wounded. The growth of any plant is thus mainly the outcome of multiplication of cells at its meristems, their subsequent increase in volume leading both to a lengthening and gradual widening of the tissues. As they reach maturity the new units mostly become specialised to serve diverse needs. Those cells, however, which have not undergone profound modification, but have retained their juvenile

character, often retain also their power of division and capacity to develop in different ways as the demands of the organism may dictate. It is the visible enlargement of plants that is popularly spoken of as growth, but in reality this involves the three phases of cell-division, enlargement, and the final differentiation which will form the subject-matter of the next chapter.

CHAPTER VII

THE DIFFERENTIATION OF PLANT-CELLS

FOUR principal types of element [1] are found in vegetable tissues. A large part of the plant-body is composed of cells which usually appear rounded or polygonal in transverse sections, and commonly contain a living protoplast. In longitudinal sections they are often rectangular in form, seldom more than two or three times as long as broad, and provided with square or rounded ends (cf. Fig. 84). Such cells, described as *parenchymatous*, frequently have thin walls, and often form extensive tissues known as *parenchyma*.

In contrast to this type are other cells, termed *prosenchymatous*, in which the length greatly exceeds the breadth, such elements being found more particularly in the mechanical and conducting tissues. These cells usually have pointed ends and thickened walls (Fig. 39, C, D), and the width, as seen in transverse section, is commonly small as compared with that of a parenchymatous element (Fig. 39, B). Occasionally forms of cells are encountered which are transitional between these two types.

The elements of the third type are of quite a different character, and are termed *vessels* (Fig. 40). They are the principal water-conducting structures in the wood of Flowering Plants, possess no living contents when mature, and their longitudinal walls are thickened in various ways (p. 67). In the mature condition they appear as long wide tubes or cylinders, but they are actually derived from vertical rows of cells by the more or less complete breaking down of all cross-walls. Perforated septa thus occur at intervals in the course of the vessel, and in woody plants are often obliquely radial with reference to the organ as a whole. The cross-walls may almost entirely disappear (as in the Maple and Oak, Fig. 40, F), but most commonly a distinct rim persists, only the central part being absorbed (*e.g.* the Lime or the Poplar, Fig. 40, E). In still

[1] These, and the various modifications described in the present chapter, are most easily studied by teasing out (*i.e.* tearing to pieces with a pair of needles) small portions of a Celery-stalk or Marrow-stem that have been previously boiled for some time in water; the middle lamellæ are thereby dissolved, so that the individual cells readily separate from one another.

other instances the walls break down in such a way that a number of cross-bars remain (*e.g.* the Alder, Fig. 40, D). The original cells are called vessel-segments.

The elements of the fourth type serve for conduction of elaborated food-materials. They are known as *sieve-tubes*,[1] and are located in the phloem, a tissue that in most stems lies just outside the wood. The sieve-tubes, like the vessels, are derived

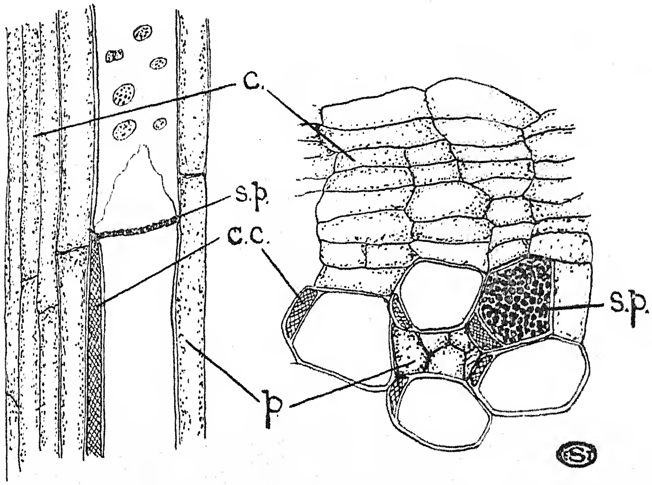

FIG. 36. Phloem-structure of the Vegetable Marrow (*Cucurbita*), in longitudinal (left) and transverse (right) sections. *c.*, cambium; *c.c.*, companion cells; *p*, phloem parenchyma; *s.p.*, sieve-plate.

from vertical rows of cells whose cross-walls are perforated by a large number of fine pores through which the protoplasts of the adjacent segments become connected. They retain their living contents in the mature condition, and the membranes remain relatively thin (Fig. 36). When the cross-walls are seen from the surface they present the appearance of a sieve, the meshes of which constitute the pores; these walls are spoken of as *sieve-plates* (Fig. 36, *s.p.*).

Before the sieve-plates are fully developed each cell divides longitudinally into two unequal portions. The larger constitutes a segment of the sieve-tube whose nucleus is stated generally to degenerate, whilst the smaller, which retains its nucleus, forms a so-called *companion cell* (Fig. 36, *c.c.*). Sometimes two, or even three, companion cells may be produced before the nucleus of the

[1] See also p. 139. Sieve-tubes of a different type occur in Ferns and Gymnosperms (pp. 372, 412).

sieve-tube segment dies away. The narrow companion cells have dense granular contents in contrast to the wider sieve-tubes, which possess but a thin lining layer of cytoplasm and a large central vacuole, features by which they are often readily recognised in transverse sections.

Behind the meristem the cells have been seen to exhibit a steady increase in size until they attain full dimensions. During the phase of enlargement the walls undergo no appreciable thickening, but surface growth takes place. This is probably accomplished by stretching of the elastic membrane and intercalation of new particles of cell-wall substance between those already present. When fully grown, more or less marked *thickening of the wall* occurs, successive layers formed by the agency of the living protoplast being deposited on the inner surface. Subsequently the wall often undergoes considerable chemical changes, as a result of which it may become more or less impermeable to water, so that the contained protoplast dies. When the thickening is at all conspicuous, the successive layers generally appear more or less distinct (Fig. 37, D; 39, B). This *stratification* is due to the fact that the layers adjacent to one another are of unequal density.

As a general rule the thickening is not uniform over the whole inner surface of the wall, small areas commonly remaining thin (Fig. 37, A). The intimate relation between adjacent cells is evidenced by the fact that such thin areas, interrupting the layers formed by the protoplast of one cell, coincide with the thin areas on the outer sides of its walls, where no thickening has been deposited by the protoplasts of the surrounding cells. In these areas, known as *simple pits*, the original middle lamella (the *pit-membrane*, Fig. 37, A, *pm.*) alone separates the adjacent cells. The majority of the protoplasmic connections (cf. p. 57) pass through these pit-membranes.

Good examples of simple pits are seen in sections of Elder pith (Fig. 37, B). In surface view they appear as more transparent oval or elliptical areas which are irregularly scattered (*Ps.*). In section (*p.*) the walls appear broken at sundry points; but careful focussing shows that the apparent gaps are really bridged by a thin line, the pit-membrane. In the endosperm of the Date (Fig. 37, A), the cotyledon-walls of the Lupine and many other Leguminosæ, and cells of the cortex of the Mistletoe, the thickening is so extreme that the cavity of the cell becomes much reduced, and the pits then appear as deep depressions within the wall. It is in such tissues that the protoplasmic connections between cell and cell can most readily be demonstrated.

The thick-walled elements of the plant are of considerable

mechanical importance, since they form skeletal tissues which are mostly devoid of intercellular spaces. When such mechanical elements occur in young growing organs, where too great a rigidity

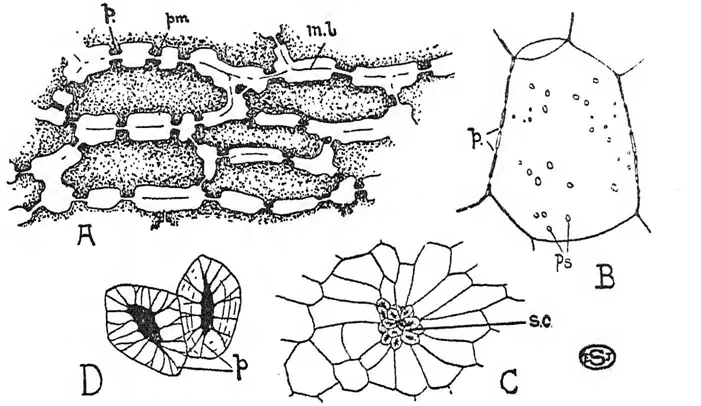

FIG. 37. Thickened cell-walls. A, Portion of the endosperm of the Date (*Phœnix*) in section. B, Pith-cell of the Elder. C, A group of stone-cells of the Pear, together with a small part of the adjacent flesh. D, Two isolated stone-cells. *m.l.*, middle lamella; *p.*, pits seen in section; *pm.*, pit-membrane; *Ps.*, pits in surface view; *s.c.*, stone-cells.

is disadvantageous, they take the form of *collenchyma* which differs from other strengthening tissues in the fact that its cells are living. Collenchyma is frequent immediately beneath the epidermis in

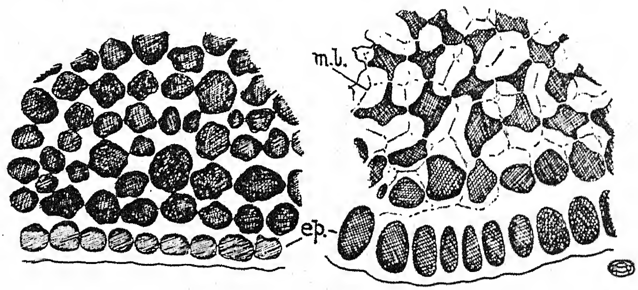

FIG. 38. Collenchymatous tissue from the stems of the Burdock (*Arctium*) (left) and Dead Nettle (*Lamium*) (right). *ep.*, epidermis; *m.l.*, middle lamella. Both in transverse section. The cell-contents are shaded.

young stems (Fig. 80, A, *s*), in the midribs of young leaves (Fig. 98, *M*), and in the adult stems of some herbs. In its most typical form it is characterised by extreme thickening of the corners of the cells, as seen in transverse section (Fig. 38), the thickened angles appearing bright and shining owing to their highly refractive character.

Sometimes, however, collenchyma exhibits uniformly thickened walls, interrupted only by pits. The thickening, unlike that of most mechanical elements, is practically unaltered *cellulose*, which possesses considerable stretching power, so that collenchyma is well suited to act as a supporting tissue in young growing organs (cf. p. 67).

All cellulose-walls [1] exhibit this character, and, moreover, are readily permeable to water. Cellulose is one of the more complex carbohydrates, belonging to the series of the polysaccharides (p. 76). It is scarcely coloured by iodine solution, but is stained blue if the application of iodine is preceded by that of strong sulphuric acid. The acid causes swelling of the wall, and this is followed by complete solution, the blue colour with iodine being due to one of the products. Cellulose-walls are likewise dissolved by ammoniated copper oxide (cuprammonia, see Appendix V). A blue colouration and swelling also results from the application of chlor-zinc-iodide (Schultze's solution, Appendix V). Useful stains for cellulose walls are methylene blue and hæmatoxylin (Appendix IV), the latter giving a deep purple colour.

The remaining mechanical elements form tissues termed *sclerenchyma*, distinguished from collenchyma by a chemical change of the thickened walls known as *lignification*, in consequence of which the cell-contents ultimately die. Such lignified walls are much harder and stronger than those consisting of cellulose. They possess relatively little elasticity, and when wet are not readily permeable to water and practically impermeable to air. The exact nature of the chemical change is not known, but it is sufficiently profound to lead to marked differences in reaction. Thus such walls are insoluble in cuprammonia, whilst the lignin is dissolved by Eau de Javelle (Appendix V) and also by sodium sulphite. Iodine solution stains lignified walls brown, and a similar colouration is obtained with chlor-zinc-iodide. Aniline chloride, or sulphate, which does not colour cellulose-walls, yields a brilliant yellow colouration and, as it does not stain starch, is particularly useful when that substance is present. An alcoholic solution of phloroglucin, followed by strong hydrochloric acid, produces a scarlet colouration. Lignified walls stain yellow or brown with hæmatoxylin, and are deeply stained by gentian violet. The latter is effective in contrast with Bismarck brown, the wood and other sclerenchyma becoming violet and the ordinary cell-walls brown.

There are two principal types of sclerenchymatous elements,

[1] Mingled with the cellulose in the walls of many plant-cells, especially those of succulent fruits (*e.g.* Apples, Gooseberries) and storage roots (*e.g.* Beetroot), are so-called pectic substances which are soluble in water.

5

viz. stone-cells and fibres; of these the former are more or less parenchymatous, the latter prosenchymatous in shape. The gritty character of the flesh of some Pears is due to *stone-cells* which, in a thin section, can be seen to occur as little clusters (Fig. 37, C) irregularly scattered through the thin-walled parenchyma forming the flesh. The cavity of each stone-cell is very much reduced and inconspicuous owing to the strong thickening of the wall (Fig. 37, C and D, *s.c.*). This shows distinct stratification, and is traversed by a number of dark lines (*p.*) radiating from the centre and branching as they approach the surface. These are the pits which serve for the transference of nourishment to the protoplast during the process of thickening, on the completion of which the living matter dies.

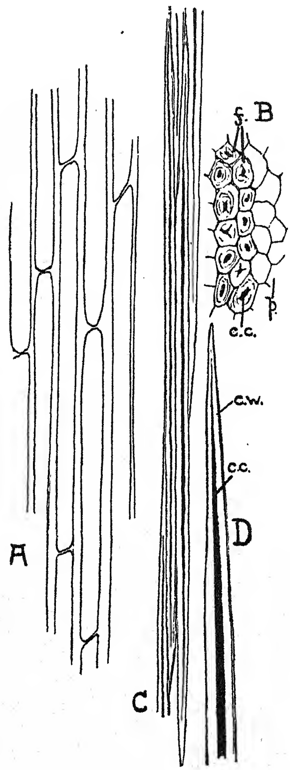

FIG. 39. Collenchyma of Dead Nettle stem in longitudinal section (A), and fibres from the stem of the Hop in transverse (*B*) and longitudinal sections (C, D). *c.c.*, cell cavity; *c.w.*, cell-wall; *f*, fibres; *p*, parenchyma.

The *fibre* is a narrow, very much elongated, cell with tapering pointed ends, and in the adult condition its protoplast is frequently dead. The walls are in general strongly thickened and lignified (Fig. 39, B–D), and usually bear a number of oblique slit-shaped pits. In the mature plant fibres are generally the most important form of mechanical element, being frequently present in the cortex and composing a large proportion of the wood of thicker branches (cf. p. 175). The cortex in the young stems of many woody plants exhibits a continuous mechanical ring composed of alternating groups of fibres and stone-cells.

Plant-fibres can undergo considerable elongation and can bear very heavy strains without losing the power of again contracting to their original length; loads as great as 14 to 25 kilogrammes are required to produce permanent lengthening. The powers of fibres in this respect may be compared with those of metal rods (*e.g.* of wrought iron and steel) which, whilst they become permanently stretched under similar strains, exhibit far less extension before the limit of their

elasticity is reached. Fibres will thus permit bending on the part of a plant-organ (under the influence of the wind, for example), and will not give way, even under considerable strain; moreover, their elasticity will bring about a return to the normal position as soon as the strain is relieved. Whilst the breaking strain (10–12 kilogrammes) for collenchyma is not much less than that for many fibres, it exhibits permanent elongation under quite low tension, so that it is especially suited to the mechanical needs of a growing organ where constant extension is taking place.

Owing to their great strength, fibres of sufficient length for spinning are used for the manufacture of textiles, rope, etc. They are usually prepared from herbaceous plants by removing the softer tissues or allowing them to rot away. Important fibre-yielding plants [1] are the Flax (*Linum usitatissimum*), in which the fibres may attain a length of over 50 mm., New Zealand Flax (*Phormium tenax*), Hemp (*Cannabis sativa*), and Jute (species of *Corchorus*, mainly cultivated in Bengal). Manila hemp used for high quality ropes is obtained from the leaves of a Banana (*Musa*) cultivated in the Philippines, while Sisal hemp is made from the fibres of a species of *Agave*. Coir, used mainly for matting, etc., is derived from the Coconut, whilst Raffia-tape or bast is obtained from the Palm *Raphia*.[2] Moreover, fibres treated in various ways are the source of wood-pulp and other paper-making materials.

The main function of *vessels* (Fig. 40) is water-conduction, but they also assist in mechanical support on account of their thick walls. These are necessitated by the frequent existence of negative pressures (p. 203) in the water-conducting tracts, such as obtain, for instance, when transpiration is active. At these times collapse of the vessels, under the positive pressure exerted by the surrounding elements, is prevented by the rigidity of the vessel-walls. The type of thickening varies greatly, depending largely on whether the vessel is formed in a part of the plant that is still growing or in one that has reached maturity. In the former the thickening must be of such a nature as to admit of stretching of the wall, which would otherwise be ruptured.

The first-formed vessels of the wood (*protoxylem*), which differentiate a short distance behind the meristem, exhibit continuous spirals or disconnected rings of thickening (*spiral* and *annular* vessels, Fig. 40, A, B). These are deposited on the inner side of the original vessel-wall, to which, however, they are often

[1] Regarding these and other economic plants, see R. Good, *Plants and Human Economics*, Cambridge University Press, 1933 (202 pp.); A. F. Hill, *Economic Botany*, McGraw Hill Book Co., 1937 (592 pp.); also the work of Lindley and Moore, cited on p. 603.

[2] Regarding cotton, see p. 159.

only attached by a narrow connection, as can be seen in optical section (Fig. 40, C). As the organ elongates the spirals are drawn out like a spring, and the rings become more widely separated, by the gradual stretching of the unthickened part of the wall. If, however, growth in length is very considerable (as, for instance, in many Monocotyledons and aquatics), complete rupture may ultimately take place, so that in the mature plant only an irregular

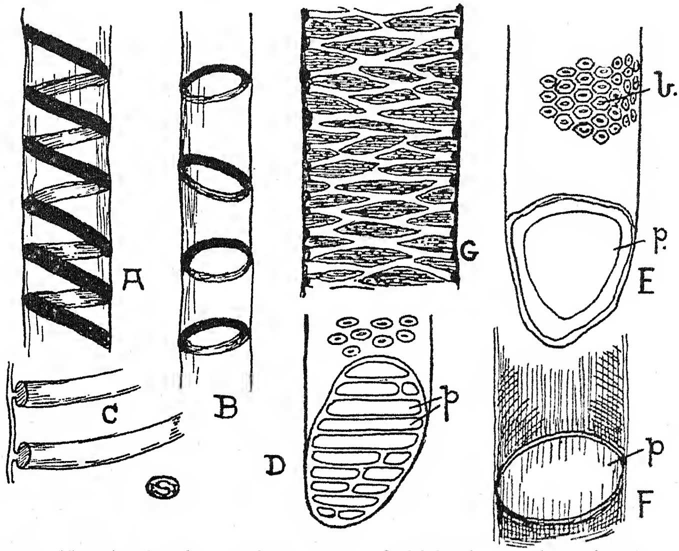

FIG. 40. Vessels showing various types of thickening and perforation. A, spiral; B, annular; C, portion of A in longitudinal section showing attachment of thickening to wall; D, end of vessel of Alder (*Alnus*) showing ladder-like perforation; E, vessel of Poplar (*Populus*); F, vessel of Oak (*Quercus*); G, reticulate vessel of Marrow (*Cucurbita*). *b.*, bordered pit; *p.*, perforations between segments of vessel.

canal remains to indicate where the protoxylem was situated (Fig. 85, A, *P.c.*).

The vessels formed after completion of growth often exhibit *reticulate* thickening (Fig. 40, G), which appears as a more or less irregular network of ridges deposited on the inner side of the original wall. Careful examination shows that the meshes of this reticulum often possess the characters of bordered pits.

Such *bordered pits* are very common on the vessels in the older wood. An examination of the surface of the vessel wall under the high power of the microscope shows that each pit is provided with a broad *border* (Fig. 40, E, *b.*; also Fig. 41, B, *b*). This is either circular in outline, or more commonly polygonal when the pits are

crowded, the actual aperture of the pit appearing round (Fig. 41, B, *p*) or more or less slit-shaped. In section the border is recognised as a dome-shaped cover formed by the thickening of the wall, which around the pit arches away from the middle lamella (*i.e.* pit-membrane); the top of this low dome is perforated by the aperture leading into the pit (cf. also Fig. 280, D, p. 413). Where two vessels adjoin one another, such a perforated dome

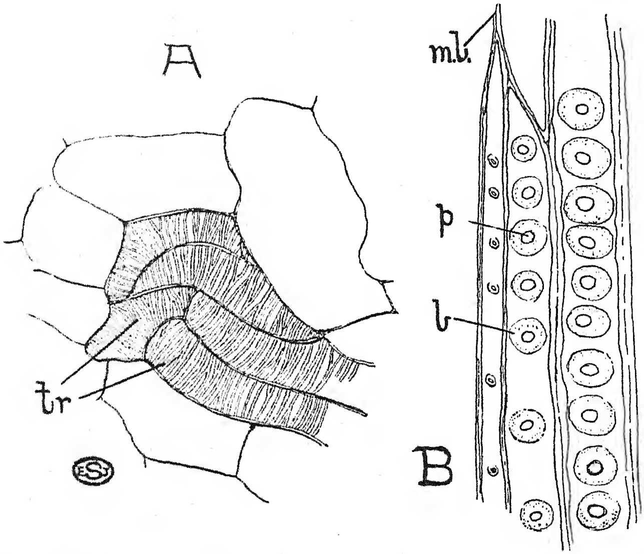

FIG. 41. Tracheids. A, Spiral type, from the leaf of Dog's Mercury (*Mercurialis*). B, Bordered-pitted, from the stem of the Scot's Fir (*Pinus*). *b*, border of bordered pit; *m.l.*, middle lamella; *p*, aperture of bordered pit; *tr.*, tracheids.

occurs on either side of the common wall, so that these bordered pits coincide. The pit-membrane may possess a central thickened area (*torus*) which, owing to its modified character, is impervious alike to air and water.

When the pit-membrane, which is easily displaced, is forced to one side or the other, the torus closes up the aperture of the dome, and thereby any passage of water or of air from one vessel to the other is prevented. Such displacement will occur when the pressure in one vessel differs from that in the adjacent one, so that the bordered pits operate as safety-valves whereby differences of pressure in the wood become localised.

The conduction of water in the higher plants is mainly effected by means of vessels, but another kind of conducting element, the

tracheid, which is likewise dead, is also found in the wood of thicker branches and, more commonly, in leaves. Each tracheid is formed from a *single* cell which is more or less elongated in form, and usually bears bordered pits (Fig. 41, B) or spiral thickening (Fig. 41, A). The wood of the Fir and other Conifers is entirely made up of long tracheids, similar in appearance to fibres, but bearing pronounced bordered pits (Fig. 41, B). Very narrow bordered pits appearing as oblique slits are not uncommon in wood fibres.

The walls of mature cells often undergo chemical changes other than lignification, some of which (*e.g.* the change affecting the cells of the cork, p. 186) will be described later, but a few special instances may conclude the present chapter. In a number of plants the thickening of the walls of certain cells takes the form of layers of *mucilage* of varying chemical constitution. These, in the dry condition, are hard and horny, but in the presence of moisture they soften and swell up considerably. Indeed, such mucilaginous walls possess a remarkable power of absorbing and holding water, and are particularly prevalent in plants characteristic of dry situations. The slimy character of many Seaweeds is due to the mucilaginous nature of nearly all the cell-walls, and here the change in bulk, as between the dry and wet condition, is especially evident. Mucilaginous walls stain deeply and rapidly with aniline blue.

The *gums* formed by certain plants are probably very similar chemically to the mucilages, and, like them, often appear to arise as a result of chemical alteration of the cell-wall. Diverse species of *Acacia* yield gums of economic importance, *e.g.* gum arabic (from *A. senegal*), catechu used in tanning (from *A. catechu*), etc.; gum tragacanth, which is far less soluble, is obtained from species of *Astragalus*.

Another frequent modification consists in the deposition of mineral substances within the cell-wall. For example, in the Horsetails (*Equisetum*) and most Grasses the membranes of the outer cells are impregnated with silica, to which many Grass-leaves owe their sharp cutting edges. This *silicification* increases the stability of the plant and also serves as a protection against snails, etc. A siliceous envelope is very characteristic of certain minute unicellular Algæ known as Diatoms (cf. p. 294).

Sometimes the surface of the plant is encrusted with carbonate of lime, as in some Stoneworts (*Chara*) and certain other lowly members of the Vegetable Kingdom (cf. p. 292). Local deposits of lime on special ingrowths of the walls are not uncommon in the epidermal cells in certain Flowering Plants. The resulting struc-

tures are known as *cystoliths*, and are well seen in the leaves of the Stinging Nettle (Fig. 42, *C*) and of various kinds of Fig (*e.g.* in *Ficus elastica*). If sections of the leaves are placed in weak acetic acid, the carbonate of lime dissolves with effervescence and the framework of the cystolith becomes visible.

In the mature plant the different types of elements are grouped

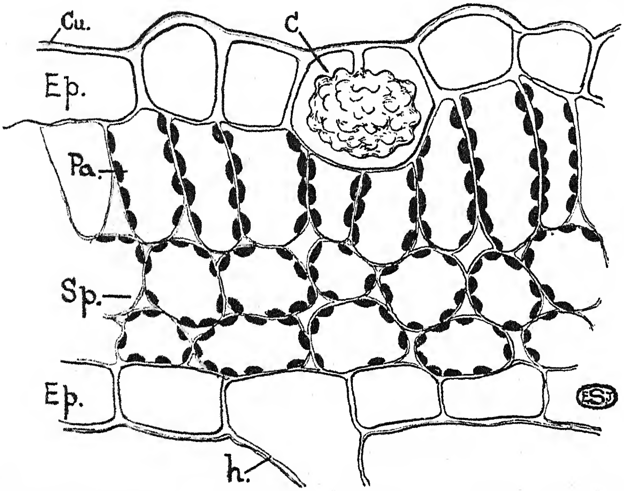

FIG. 42. Transverse section of the leaf of a Nettle (*Urtica*) showing a cystolith (*C*). *Cu.*, Cuticle; *Ep.*, epidermis; *h*, hair; *Pa.*, palisade tissue; *Sp.*, spongy parenchyma.

together to form *tissues* subserving diverse functions. Thus, for instance, one tissue, which is always superficial and has the general function of protecting the underlying parts, constitutes the epidermis. The vascular tissues, comprising the wood or xylem and the phloem, form the principal conducting systems for water and mineral salts, and for elaborated food-substances, whilst others —largely parenchymatous in character—go to form the general matrix or ground tissue. It must not be supposed, however, that, because there is one general function, the component elements of these and other tissues are necessarily uniform in character.

CHAPTER VIII

FOOD-RESERVES AND ENZYMES

APART from the living constituents, cells usually contain numerous substances which are either dissolved in the sap or, when insoluble, occur as solid bodies or suspended drops. These substances can for the most part be grouped as food-bodies or as by-products, according as they are known to be employed in the nutrition of the plant or are supposed to be of no further nutritive value.

Among the commoner *food-substances*[1] are various carbohydrates (*e.g.* sugars, starch, etc.), oils, and proteins, all of which have been built up by the plant from simple inorganic compounds by a series of complex changes. During the earlier part of the season such food-substances are used directly to supply the necessary materials for growth, but subsequently, with decreasing demands, a large proportion are stored up for future use. In perennial herbs they accumulate in those organs which persist from year to year (*e.g.* bulbs, tubers, etc.), whilst in woody perennials they are stored in the stem- and root-systems (see p. 226). Similar food-substances are, moreover, laid up within the cotyledons or endosperm of all seeds. Carbohydrates are organic compounds built up of the elements carbon, hydrogen and oxygen, the last two being present in the same ratio as in water. Oils have an analogous composition but contain proportionately less oxygen. Proteins are far more complex containing, in addition to carbon, hydrogen and oxygen, the elements nitrogen and sulphur.

One of the most important food-substances is *starch*, which is insoluble in the cell-sap and is often the first easily recognisable product of photosynthesis. On microscopic examination the starch appears as very small shining grains, mainly within the chloroplasts (Fig. 26, *St.*). These grains gradually increase in amount during the day, but generally disappear over-night, and are consequently spoken of as *transitory starch.* Their gradual accumulation on a bright day is due to the conversion of the soluble sugars, produced more rapidly than they can be removed, into insoluble starch. In

[1] For reference-books, see p. 97.

darkness, when photosynthesis ceases, the accumulated starch is changed back into sugar and transferred to other parts of the plant.

In contradistinction to this transitory starch, that which accumulates in storage-organs usually takes the form of rather large grains which originate within colourless plastids, known as *leucoplasts.* The latter occur in those cells which are not exposed to light, and differ from chloroplasts only in the absence of chlorophyll, which is generally not produced in darkness. Leucoplasts, however, readily change to chloroplasts. When a Potato-tuber, for instance, is exposed to light, it turns green through the formation of chlorophyll within the leucoplasts. Large starch-grains may actually be produced within green plastids (*e.g.* in a greenhouse plant, *Pellionia*), and these provide particularly appropriate material for studying the mode of formation of the grains.

In a transverse section of the stem of *Pellionia* the outermost cells (Fig. 43, *a*) are seen to contain chloroplasts (*ch.*), in some of which there is a bright shining dot, the transitory starch-grain (*s*). The larger starch-grains, seen nearer the centre in various stages of development, may be supposed to have originated likewise, as small bodies within the chloroplasts there situated (Fig. 43, *b*). But in the mature condition these grains have enlarged to such an extent that the enveloping chloroplasts appear merely as green caps to one side of them (Fig. 43, *c*, *ch.*).

The large starch-grains that can be scraped out of a Potato are more suitable for the study of details of structure. Examined in a drop of water, each shows a number of asymmetrical layers arranged around the darker *hilum*, or point of origin (Fig. 43, *d*). This stratification indicates the manner of growth of the starch-grain, the successive layers being distinguished, presumably, by differences either in chemical or physical structure. In the grains of the Potato (Fig. 43, *d*) and *Pellionia* (Fig. 43, *c*) the point of origin is towards one end (*excentric* type). On the other hand, the hilum, in those from the cotyledons of the Pea or Bean, lies in the centre (*centric* type, Fig. 43, *f* and *g*), and the layers are arranged symmetrically around it. The dry grains of Pea, Bean, etc., exhibit a number of radiating cracks, which appear as dark irregular lines (Fig. 43, *g*); these seem to be due to the drying up of some of the imbibed water which permeates the substance of all starch-grains.

Whilst most of the grains of Potato-starch show but a single hilum, an occasional one will be found to possess two or three, each with its own system of layers (Fig. 43, *e*). This results from the development of several grains within the same leucoplast,

growth of each occurring independently until they meet; deposition of starch sometimes continues with the formation of layers common to the whole group (Fig. 43, *e*). Such structures are called *compound grains*. In many cereals numerous grains arise in

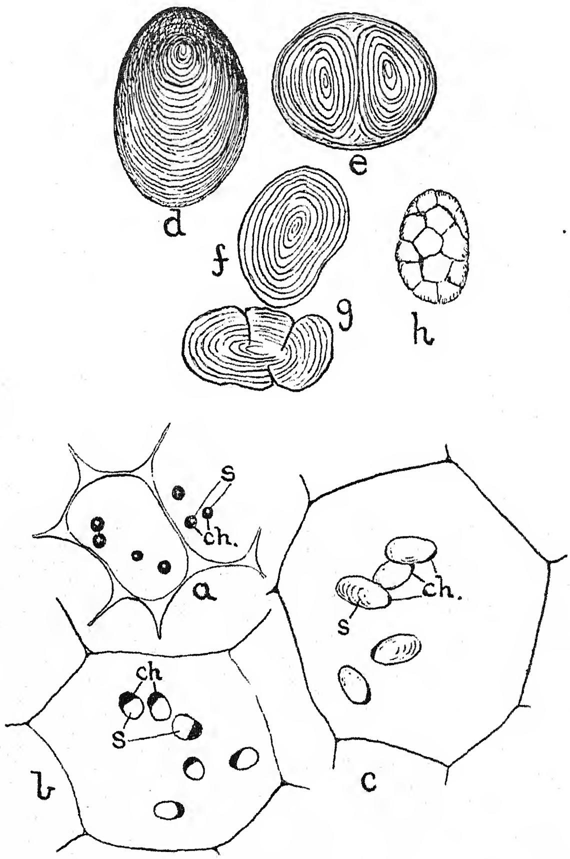

FIG. 43. Starch-grains. *a–c*, Stages in the development of grains within the chloroplasts of *Pellionia*; chloroplasts shown black. *ch.*, Chloroplasts; *s*, starch-grains; *d* and *e*, Potato starch; *f* and *g*, Pea starch; *h*, Compound starch-grain of Rice.

each leucoplast, so that the compound structure may even consist of numerous units. Thus a starch-grain of the Rice (Fig. 43, *h*) or Oat is marked out into a number of small areas, each representing a constituent unit.

Starch-grains have been regarded as consisting of at least two substances, an outer layer composed of amylopectin and an inner layer consisting of the poly-

saccharide (cf. p. 76) amylose; these occur approximately in the proportions of two to one. The two constituents may be separated by the treatment of starch with dilute caustic soda or by the action of enzymes (p. 83). Amylopectin is composed of a carbohydrate-complex in combination with phosphoric acid, whilst amylose is a pure carbohydrate. Starch and cellulose both consist of a large number of glucose-units linked together by atoms of hydrogen and oxygen, but with differing orientation in the two substances. When boiled with water, starch-grains swell and provide a starch-paste or an opalescent "starch-solution," which is considered to be a solution of amylose thickened by a gelatinous suspension of amylopectin. This "solution" is colloidal in character, and therefore will not diffuse through an organic membrane. Examination with X-rays appears to indicate that starch-grains have a crystalline structure. Under polarised light they exhibit a black cross with the hilum as its centre. Comparatively few dyes colour starch, although gentian violet and eosin are notable exceptions.

The accumulation of starch-reserves by plants is a feature of the greatest economic importance, constituting as they do a very important article of human diet.[1] The cereals, the pulses, and Potatoes, all of which contain a high percentage of starch (cf. p. 83), furnish a sufficient illustration. Cereals [2] are the fruits of Grasses; of these the most widely consumed are Rice (*Oryza sativa*), Millet (*Pennisetum typhoideum*, *Sorghum*, *Panicum*, *Setaria*), and Maize (*Zea mais*), cultivated in tropical countries, whilst Wheat (*Triticum*), Oats (*Avena*), Barley (*Hordeum*), and Rye (*Secale cereale*) are grown in temperate climates. Tapioca is obtained from the root-tubers of the Cassava or Mandioc (*Manihot utilissima*, a member of the Spurge family, widely grown in the Tropics), whilst sago is the starch found in the pith of various Palms (mainly species of *Metroxylon*, cultivated in the Malay region), from which it is extracted after the appearance of the inflorescence. Buckwheat (*Fagopyrum*, Polygonaceae) is used as a chicken-food.

The wide distribution of starch as a form of storage of carbohydrate material can probably be related to its insoluble character, in consequence of which it exerts no osmotic pressure. The small amount of moisture in seeds renders them unsuited to the storage of soluble carbohydrates, and doubtless explains the frequent occurrence of starch in the endosperm and cotyledons. In succulent storage organs, on the other hand, soluble carbohydrates often occur. One of the most important is *inulin*, another of the complex polysaccharides, with a molecular weight which, though smaller than that of amylose, is still large. As a result, in spite of its solubility and frequent high concentration, inulin has but little effect on the osmotic pressure of the cells containing it (cf. p. 46).

Inulin is found especially in the Compositæ and the allied family of the Campanulaceæ, but also in the bulb of the Wild Hyacinth (*Scilla nutans*) and in other Monocotyledons. Soluble

[1] See the reference-books, listed on p. 67.

[2] Of these cereals there are many races in cultivation which differ not only as to their yield, their resistance to climatic extremes and to diseases, but also as to their properties. Thus some Wheats, grown chiefly in continental climates, produce a high proportion of gluten and yield "strong" flour.

carbohydrates of a similar chemical constitution are, moreover, encountered in many members of the latter group (*e.g.* the graminin of Grasses, the irisin of the Iris, etc.).

In a fresh tuber of the *Dahlia* or Jerusalem Artichoke (*Helianthus tuberosus*), the intact parenchymatous cells contain inulin dissolved in the sap. On placing relatively thick sections in spirit, the inulin is deposited as a finely granular precipitate. In material kept for some weeks in spirit, so that the latter has only penetrated slowly into the tissues, the inulin will be found as big spherical or lobed masses deposited on the cell-walls. These *sphere-crystals* (Fig. 44, *In.*) usually show concentric layers, whilst radial lines

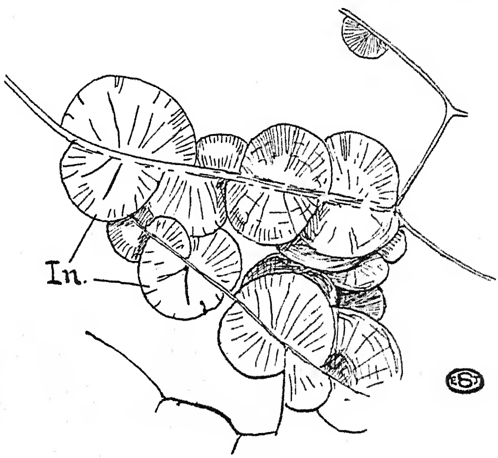

FIG. 44. Sphere-crystals of inulin (*In.*) in the cells of the tuberous root of a Dahlia.

traversing them indicate the numerous component needle-like units. On warming in water, the sphere-crystals of inulin readily dissolve. Sections treated with orcin (in alcohol), followed by concentrated sulphuric acid, acquire a deep orange-red colour.

Sugars are among the most important of the soluble carbohydrates present in plants. They possess much simpler molecules than the polysaccharides just considered, being either monosaccharides with the general formula $C_6H_{12}O_6$, or disaccharides with the formula $C_{12}H_{22}O_{11}$. Disaccharides and polysaccharides are so called since they respectively split up, under certain circumstances, into two or many molecules of monosaccharides.

Among the *monosaccharides* found in plants, the commonest are dextrose or glucose (popularly known as grape-sugar) and fructose or levulose (fruit-sugar), whilst of the *disaccharides* sucrose or

saccharose (cane-sugar) and maltose (malt-sugar) deserve mention. Owing to their relatively simple molecules they produce a high osmotic pressure, although for solutions of equal strength this is greater for monosaccharides than for disaccharides. For this reason no doubt grape-sugar and cane-sugar, the two which function as food-reserves, are only found in very minute quantities in seeds (except for the cane-sugar in the Sweet Corn, a variety of Maize). On the other hand, grape-sugar is one of the principal carbohydrate-reserves in the bulb of the Onion, whilst cane-sugar occurs in the Sugar Beet (*Beta*), in the pith of the stem of the Sugar Cane (*Saccharum officinarum*), and in the Sugar Maple (*Acer saccharinum*) (see p. 177). The sugar is extracted from the sliced Beet with the aid of warm water, whilst in the Sugar Cane the juice is crushed out of the canes with the help of rollers. In both the crude sugar is subjected to subsequent processes of refinement. The impure uncrystallisable residue is known as molasses.

Fructose is most abundant in succulent fruits, and is an important constituent of nectar; in both, however, it is mixed with, usually smaller amounts of, grape and cane sugars. Such sugars are, of course, not of the nature of food-reserves, but serve a biological purpose in connection with seed-dispersal and pollination.

All the four sugars above mentioned are found in foliage-leaves, though in proportions that vary greatly both during the day and night and at different seasons of the year. It is still an open question whether glucose or sucrose is the first sugar to be formed in photosynthesis; but there is no doubt that the other two, like the transitory starch, are secondary products. *Maltose* appears to be produced invariably during the solution of starch within the plant, and is consequently found not only in foliage-leaves, but in germinating Barley (malt) [1] and other starch-containing seeds. The fructose found in leaves, on the other hand, is formed by the breakdown of cane-sugar.

Cane-sugar is readily split (in the presence of water, so-called hydrolysis) into two molecules of monosaccharide by boiling the solution with a few drops of some mineral acid (*e.g.* hydrochloric acid); one molecule of glucose and one of fructose are obtained, the mixture being known as *invert sugar*. Cane-sugar is similarly converted into invert sugar by the agency of an enzyme *invertase* found in most plants. In the same way the polysaccharides above discussed can be split up with the formation of disaccharides or

[1] The malt is obtained by allowing moistened Barley to germinate at a moderate temperature, after which the latter is raised so as to kill off the Barley, the conversion of starch into sugar continuing owing to the presence of diastase (see below).

monosaccharides, as the case may be. For instance, a starch "solution" boiled with a few drops of a mineral acid becomes clearer, and the ordinary reaction to iodine gradually disappears; the colour assumed with this reagent is now reddish, owing to the presence of simpler polysaccharides known as *dextrins*. If the boiling be continued, the whole of the starch "solution" ultimately breaks down into glucose. Similarly inulin gives rise to fructose. In the plant starch and inulin are acted upon by enzymes, *diastase* and *inulase* respectively, which effect like changes, except that diastase breaks down starch into the disaccharide maltose, which in its turn is acted upon by an enzyme *maltase* with the production of two molecules of glucose.

The sugars are readily distinguished from one another by certain characteristic reactions. Thus glucose, fructose, and maltose all reduce Fehling's solution (which contains cupric oxide, Appendix V) with the formation of a red precipitate of cuprous oxide, and are consequently known as reducing sugars. Sucrose, on the other hand, is a non-reducing sugar, giving no precipitate with Fehling's solution, until it has been inverted by boiling or enzyme-action. It may be added that neither inulin nor the dextrins effect reduction of this reagent.

For microchemical purposes, especially when but small quantities of sugars are present, the following procedure is more advisable. The sections are mounted in a drop of a solution of phenylhydrazine hydrochloride (Appendix V) in glycerine with which a drop of a solution of sodium acetate in glycerine is thoroughly mixed. The preparation is heated for about half an hour (although a longer period is often necessary) and allowed to cool. The phenylhydrazine reacts with many of the sugars to form insoluble yellow crystalline compounds, known as *osazones*. Glucose and fructose produce the same osazone, whose crystals appear as long needles arranged in sheaves (Fig. 45, A); that of maltose forms rosettes or plates of broad needles (Fig. 45, B), whilst cane-sugar produces no osazone.

Another method of storage of carbohydrate-material takes the form of strongly thickened cell-walls (cf. p. 63 and Fig. 37, A), as in many seeds (Date, Lupine, Coffee, etc.). Such walls consist of so-called *reserve-celluloses*, polysaccharides which differ somewhat from ordinary cellulose and break down more readily into simple sugars.

Of very common occurrence in plants are complex compounds known as *glucosides*, most of which consist of glucose combined with one or more aromatic or other organic substances. On boiling with dilute mineral acids they split up into their constituents (hydrolysis). The decomposition of the glucoside within the plant is effected by special enzymes which generally occur in distinct cells, so that the chemical process is not initiated until, for some reason (*e.g.* injury), enzyme and glucoside come into contact. Thus a glucoside amygdalin occurs in the seeds of the Bitter Almond (but not in the cultivated form), whilst the appropriate enzyme *emulsin* is situated in the skin; on crushing the seeds decomposition of the amygdalin into glucose, benzaldehyde, and prussic acid takes place, this last being responsible for the poisonous properties. The hot

taste of many members of the Cruciferæ (*e.g.* Horse Radish, Cress) is due to the formation of mustard oil (together with glucose and potassium hydrogen sulphate) by the action of an enzyme *myrosin* on another glucoside *sinigrin* (myronate of potash).

In the two instances just given the glucosides undoubtedly render the plant distasteful to animals, but often they seem to serve as a means of storing glucose in a form which does not diffuse readily. Thus the leaves of many Willows contain a glucoside salicin which, during the night, is split up by the enzyme *salicase* into glucose and saligenin; the former is removed, whilst the latter combines with the new sugar formed the next day. To the glucosides also belong:—the saponins found in the Soapwort (*Saponaria*), *Quillaia*-bark, and many other plants, and easily recognised by the formation of a froth when shaken up with water; the active principles of the Foxglove (*Digitalis*), the most important being digitalin, which has a profound effect on the action of the

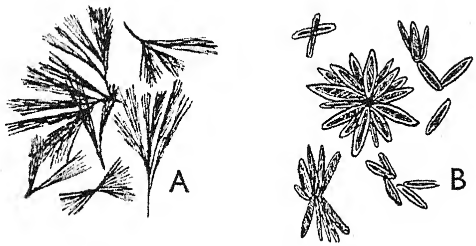

FIG. 45. Osazones. A, of glucose; B, of maltose (after Plimmer).

heart; and the indican of the Woad (*Isatis tinctoria*) and of the Indigo-plant (*Indigofera*), the latter being the source of natural indigo.[1]

Oils or *fats* constitute another important group of reserve-substances. They are formed from carbohydrates and are found especially in those seeds in which the latter are either scanty or absent (*e.g.* Castor Oil, Sunflower, etc.). Drops of oil are, however, not uncommon in the ordinary vegetative cells. The vegetable fats are compounds (esters) of glycerine with various fatty acids (palmitic acid, oleic acid, etc.), and are decomposed by enzymes known as *lipases* into their two constituents. They occur widely as fluids, although the fat of the Cocoa (*Theobroma cacao*), the so-called Cocoa-butter, forms an exception to this. In correspondence with their low specific gravity, fats are a frequent form of non-nitrogenous food-reserve in seeds depending on wind-dispersal.

The oil appears in the cell-sap or protoplasm as shining globular drops of varying size which are readily soluble in ether, benzene, etc.; some are even soluble in alcohol (*e.g.* those in the seeds of the Castor Oil). When a considerable quantity of fat is present (*e.g.* in the Brazil-nut), it can be squeezed out

[1] Vanillin, the cause of the aroma of Vanilla (obtained from the pod of *Vanilla planifolia*, a tropical Orchidaceous climber), is an aldehyde, similar to those often combined with glucose to form glucosides.

by pressure on to a piece of filter-paper, producing a greasy mark. The oil-globules turn pink or red on treatment with Scharlach Red (Appendix V), and assume a blackish colouration with osmic acid, which, however, also stains proteins and tannins. If sections of oil-containing material be placed in a solution of concentrated potash and ammonia in equal proportions, the globules after some time lose their sharply defined outline, and often become replaced by needle-shaped crystals. The change, spoken of as saponification, is due to the breaking up of the oil into glycerine and the fatty acid, the latter uniting with the alkali to form the corresponding salt.

Many plant-fats are of considerable economic importance; thus, olive oil is obtained from the fleshy fruit-wall of the Olive (*Olea europæa*, mainly cultivated in the Mediterranean region); coconut oil, used in the preparation of margarine, from the ripe seeds of the Coconut Palm (*Cocos nucifera*) [1]; Castor Oil from the seeds of the Castor Oil plant (*Ricinus communis*); and Palm Oil from the African Palm (*Elæis guineensis*). Cotton-seed is an important source of oil used largely in the manufacture of oil-cake, whilst the "drying oils" used in the paint industry are also obtained from the seeds of plants, such as Linseed (*Linum usitatissimum*), Sunflower seed, Poppy seed, or the fruits of *Aleurites* (tung-oil). Pea-nuts (*Arachis hypogæa*, with 38–50 per cent. of oil), and Soja-beans (*Glycine* spp.) are also important sources of oil. The oil is often extracted after crushing, the ultimate residue forming so-called "oil-cake," which is extensively used for the feeding of cattle. Various vegetable oils are, moreover, employed in the manufacture of soap.

The carbohydrates or fats found in the various storage-organs are always accompanied by nitrogenous food-reserves, the most important and widespread of which are the *proteins*. We have already seen that very complex combinations of proteins are organised to form the living protoplasm, but simpler proteins often occur as non-living constituents of the ordinary vegetative cells, and are especially abundant in the diverse storage-organs. In the former they may either be dissolved in the cell-sap or appear as crystal-like bodies, termed *crystalloids*, which may even be lodged in the plastids or nuclei. Succulent storage-organs, such as tubers, often likewise contain dissolved proteins, or these may take the form of crystalloids, as in the outer layers of a Potato; but not uncommonly a considerable part of the nitrogenous matter in these is a mixture of simpler compounds known as *amides* (*e.g.* asparagin in the Potato and glutamin in the Beetroot).

In seeds proteins generally occur as small grains which are well seen in the cotyledons of a Pea or the endosperm of the Castor Oil. If a section of the former be treated with iodine, the minute protein granules take on a brown colouration, in sharp contrast to the blue or blackish starch-grains with which they are intermingled. On warming a section in a few drops of Millon's reagent (Appendix V), the whole assumes a brick-red colour which microscopic examination shows to be due to the proteins. Heating with concentrated

[1] Copra is the commercial name for the dried kernel of the Coconut.

nitric acid gives a yellow colouration which, on addition of ammonia, changes to orange (xanthoprotein reaction).

The proteins of oil-containing seeds (*e.g.* Castor Oil, Brazil-nut) occur in the form of especially large granules, known as *aleurone grains*. These appear to arise, as the seed dries during ripening, from the entire contents of vacuoles rich in protein-substance. Although the structure of aleurone grains is relatively complicated, they exhibit the characteristic protein-reactions mentioned above. If a thin section of the Castor Oil or Brazil-nut (from which the fat

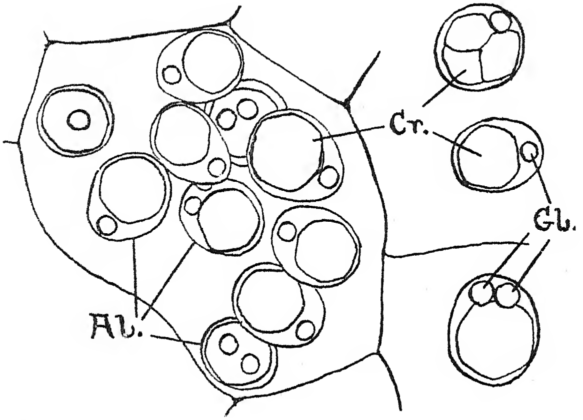

FIG. 46. Aleurone grains (*Al.*) from the endosperm of the Castor Oil plant (*Ricinus*), showing the globoid (*Gl.*) and crystalloid (*Cr.*).

has been removed by soaking in alcohol and benzene respectively) be stained with iodine, the brown-coloured grains are readily seen under the microscope. Each shows a bounding membrane, the original membrane of the vacuole, enclosing amorphous protein in which two or more bodies are embedded. One of these, the crystalloid (Fig. 46, *Cr.*), is large and more or less angular, whilst the other, the globoid, is smaller and rounded (Fig. 46, *Gl.*); both consist of protein, but in the globoid, of which more than one may be present, this is combined with a double phosphate of calcium and magnesium. By mounting sections in water the amorphous ground-mass of the aleurone grain may be dissolved, and the bounding membrane rendered clearly visible; on the other hand, treatment with dilute potash causes both bounding membrane and crystalloid to swell and disappear.

The protein-granules of the Pea, Bean, etc., are often regarded as small aleurone grains devoid of crystalloid and globoid. Similar structures occur in abundance in the so-called aleurone layer found

at the periphery of the endosperm of Grasses (Wheat, Maize, etc.), just within the coat of the grain (Fig. 47). When the latter is detached, the protein-containing layer generally comes away with it, hence the greater nourishing properties of wholemeal bread as compared with that manufactured from white flour. For the same reason peeled potatoes are not so nutritious as those boiled in their skins, since the outer layers of the tuber contain protein-crystalloids (cf. above).

Proteins, owing to their complex molecules, are not readily diffusible, and consequently become converted into simpler, freely-diffusing compounds before they are transferred to parts where

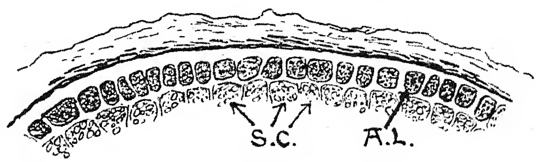

FIG. 47. Aleurone layer (*A.L.*) of Wheat as seen in a transverse section. The starch-containing cells (*S.C.*) lie immediately beneath.

growth is occurring (*e.g.* in a germinating seed). This conversion is brought about by so-called *proteolytic enzymes* (*e.g.* pepsin, erepsin), which are in general similar to those occurring in the digestive tracts of animals, although some uncertainty exists as to the exact nature of those present in plants. The chief compounds produced, by the action of these enzymes on proteins, are firstly peptones and subsequently *amino-acids*. The former still exhibit the general characteristics of proteins, although they diffuse more easily, while the latter no longer possess protein-properties. Amino-acids are exceedingly common in growing and other parts of the plant (*e.g.* leucin in the buds of the Horse Chestnut, tyrosin in seedlings of the Lupine, etc.).

Digestive enzymes are secreted by the surface of the cotyledons of endospermic seeds whereby the food-substances in the endosperm are changed into a diffusible form. In general there is no differentiation of a special secreting layer, although in Grasses the palisade-like epidermal cells of the cotyledon, in contact with the endosperm, are glandular in character. These same cells are also concerned in the absorption of the digested food-substances.

APPROXIMATE FOOD-CONTENT OF VARIOUS PLANT-PRODUCTS

(In percentages of the fresh weight)

	Starch.	Fats.	Proteins.[1]
Cocoa	4·2	50·4	13·3
Maize	68·4 [2]	4·5	9·8
Oat	58·0 [2]	5·2	10·4
Rice	75·0	0·5	9·0
Wheat	67·9 [2]	1·8	12·3
Potato-tubers . .	20·0	0·15	1·9
Lettuce	2·2	0·3	1·4
Broad Bean . . .	48·0 [2]	1·6	23·0
Pea-nuts	5·2	44·0	30·0

In view of the great importance of *enzymes* in the activities of the plant, the present chapter may be concluded with a brief consideration of their mode of action. It should be realised that such substances are probably of universal occurrence in living cells. A very large number of enzymes are now known, and others are continually being discovered, but only a few can be mentioned here. The following table gives an epitome of some of the principal enzymes found in plants:

Enzyme.	Substance acted upon.	Products.
Diastase.	Starch.	Dextrin and Maltose.
Maltase.	Maltose.	Glucose.
Invertase.	Cane-sugar.	Glucose and Fructose.
Inulase.	Inulin.	Fructose.
Cytase.	Reserve-cellulose.	Mannose and Galactose.
Emulsin, Myrosin, etc.	Glucosides.	Glucose, etc.
Lipases.	Oils.	Glycerine and Fatty Acids.
Proteases (proteolytic enzymes).	Proteins.	Peptones and Amino-acids.
Zymase (in Yeast, p. 340).	Monosaccharides.	Alcohol and Carbon Dioxide.

Diastase is readily obtained from germinating Barley (the malt of breweries). If some malt be ground to a fine powder and then shaken up thoroughly with water, a solution of the diastase is obtained. To eliminate other dissolved substances about a pint of alcohol is slowly added to about 25 c.c. of the filtered solution; the diastase is slowly deposited as an opalescent and flocculent precipitate. The clear solution above is poured away, and the precipitate filtered off. On redissolving the precipitate in water a moderately pure solution of diastase is obtained, which can be purified by a further precipitation with alcohol. This method is applicable to many enzymes. The material should always be ground to a fine powder, from which an extract is made, usually with cold water; if

[1] The percentages given are mostly calculated for the entire nitrogenous organic matter. [2] Total carbohydrates.

the filtered solution is at all bulky, it will be convenient to reduce its volume by evaporation at a temperature not exceeding 50° C.

Diastase is not confined to germinating seeds, but is responsible for the change from starch to sugar wherever it is effected in the plant. In the spring, when rapid conversion of the reserve-starch stored up in the woody parts takes place, large quantities of sugars are often carried up to the developing shoots of trees and shrubs in the water-current, so that the sap which exudes in "bleeding" (p. 194) often tastes quite sweet. The action of cytase on thick cellulose walls goes on very slowly and in consequence the period of germination is greatly prolonged, as is well seen in the Date.

A solution of invertase which will invert cane-sugar is readily obtained, according to Plimmer,[1] in the following manner. A quantity (100 grams) of ordinary Yeast is ground up with about 6 grams of calcium carbonate. The resulting paste is treated with 5 c.c. of chloroform or ether (to kill the Yeast cells), and allowed to stand exposed to the air for three or four days, after which the enzyme is precipitated from the filtrate with an equal volume of alcohol. An impure solution of invertase, which will demonstrate the inversion of cane-sugar, can, however, be obtained by simply mashing Yeast in water with the addition of a little ether, and filtering off the solid matter (preferably through an asbestos filter).

Lipase can be prepared from the seeds of the Castor Oil by cutting up the endosperm into small pieces, and soaking these for a short time in a small quantity of ether in order to remove the oil. The material is then ground into a pulp with a very dilute (0·5 per cent.) solution of acetic acid, which sets free the enzyme. The insoluble matter is filtered off, washed till the filtrate gives no acid reaction, and the residue is shaken up with a small amount of water. If some of this suspension be added to a little olive oil, an acid reaction will soon be obtained due to the formation of fatty acids consequent upon the decomposition of the oil.

The preparation of proteolytic enzymes from plant-material is a matter of some difficulty and beyond the scope of this book. The action of such enzymes is, however, well illustrated by the use of peptonising powders (containing the enzyme pepsin) in rendering milk more digestible for invalids.

The action of enzymes is very often a hydrolytic one, that is to say, the compound is broken down with the addition of water, thus:

$$\underset{\text{cane-sugar}}{C_{12}H_{22}O_{11}} + \underset{\text{water}}{H_2O} = \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\text{fructose}}{C_6H_{12}O_6}\,{}^{2}$$

$$\underset{\text{inulin}}{(C_6H_{10}O_5)_n} + \underset{\text{water}}{nH_2O} = \underset{\text{fructose.}}{nC_6H_{12}O_6}$$

In other cases, however, the action appears to be different, as, for instance, that of the fermenting enzymes (cf. p. 340) and of the oxidising enzymes or *oxidases* which are in part responsible for the change in colour of the cut surface of an Apple, and of many Fungi,

[1] *Practical Organic and Biochemistry*, 2nd edit., 1918, p. 401.

[2] Although the formulæ for glucose and fructose are the same, these two compounds differ in the arrangement of the atoms within their molecules.

when exposed to air. Evidence is accumulating in support of the view that all the chemical processes depending on enzyme-action are reversible, taking place in one direction or the other according to the prevailing conditions. Thus, for example, it is believed that the building up of starch from sugar and the reverse process are both dependent on the same set of enzymes. Little is known as to their chemical nature, but all are either colloids or linked with colloidal substances, and as a consequence the rate of diffusion through parchment and similar membranes is either very slow or practically nil.

Our knowledge of this class of substances is almost entirely confined to their mode of action. The reactions influenced by enzymes are all such as require an appreciable interval of time for their completion, so that it is possible to measure their rate under any given set of conditions. One of the most important aspects of enzyme-activity is the small quantity of the enzyme necessary to bring about a pronounced chemical change; thus invertase is stated to invert 200,000 times its weight of cane-sugar. Moreover, at the end of the reaction the enzyme appears to be unaltered both as regards amount and characteristics. In both these respects enzymes resemble the so-called *catalytic agents* employed in certain chemical processes. As examples we may mention the use of small quantities of manganese dioxide to accelerate the liberation of oxygen from chlorate of potash, and the effect of traces of colloidal (finely divided) platinum, known as platinum black, in causing the explosive combination of oxygen and hydrogen at ordinary temperatures. These reactions would also take place in the absence of the catalytic agent, but with this difference, that the rate would be very much slower. Similarly, there is reason to believe that most changes brought about by enzymes would also occur in their absence, but at so slow a rate as not generally to be capable of recognition. In this connection it is well to recall that much the same effect as is produced by the enzyme can often be attained by the use of other catalytic agents (*e.g.* boiling with small quantities of mineral acids).

Although the enzyme appears unaltered at the end of the reaction, it is almost certain that combination of some kind with the substances undergoing change takes place while the process is proceeding. In view of the large surface which is presented by colloids, it is very probable that this combination is a physical one (adsorption), and it is thought by many that, in the hydrolytic enzymes, for instance, the water and the compound undergoing hydrolysis are brought into intimate contact at the surface of the ultramicroscopic enzyme particles.

Enzymes differ from most other catalysers in that each is usually only effective in accelerating one or few particular reactions (cf. p. 83), and they are, moreover, very sensitive to heat and light. The rate of the reaction is doubled or trebled with every rise of 10° C., but soon a temperature is reached (usually about 60° C.) at which most enzymes are destroyed. It may be added that heating which suffices to kill the protoplasm leaves enzymes unharmed. Strong light destroys them very quickly, an effect for which the violet end of the spectrum appears to be mainly responsible. Many chemical compounds (*e.g.* prussic acid, chloroform, etc.) arrest enzyme-action to a more or less marked degree according to their concentration. If the products of enzyme activity are not removed, a retardation of the process is at once manifest, continued action of diastase, for example, being dependent upon the removal of the maltose. Sometimes the accumulation of the products of the reaction actually exerts a poisonous effect, as, for instance, that of the alcohol produced by Yeast. Usually, however, the substances resulting from enzyme-action are removed by the plant as soon as formed.

Enzymes frequently act only in the presence of another substance, an *activator*, which is commonly a salt, acid, or alkali, although sometimes more complex. These activators differ from the enzymes in being able to diffuse through a parchment membrane, and can consequently be separated from the latter by dialysis.[1] Examples are afforded by the small quantity of acid requisite for the action of pepsin, and the necessity of the presence of certain complex phosphatic compounds for the action of the zymase of Yeast.

Just as these substances have the effect of accelerating enzyme action, so, too, there are others which exert a retarding influence, and there is every reason to believe that either the one or the other can be produced as may be required by the living cell. The rate of the reaction depends on the amount of the enzyme present, and this latter is regulated by the cell's activity. It is clear, then, that the character and vigour of catalytic activity is subject to considerable modification, and is indeed intimately related to the momentary requirements of the organism. Moreover, mixtures of enzymes may exhibit properties which are not shared by the components separately.

[1] That is to say, placing the mixture of enzyme and activator in a parchment tray floating on a large bulk of water.

CHAPTER IX

BY-PRODUCTS AND SECRETORY ORGANS

THE by-products comprise chemical compounds [1] formed during the metabolism of the plant which do not, as far as our present knowledge goes, appear to play any further part in the elaboration of food-substances. This does not, however, mean that they fulfil no useful functions in the living organism, for they may be of importance in warding off the attacks of preying animals, in the creation of attractive mechanisms, etc. Examples are furnished by the bright colouring-matters of many petals, the ethereal oils of many sweet-smelling herbs and flowers, and the vegetable acids found in such fruits as the Lemon.

One of the most widespread of the by-products is *oxalate of lime*, which may occur in practically every organ and tissue. It is produced by the neutralisation of the oxalic acid formed during metabolism and, being insoluble, appears as crystals which assume diverse forms. Large *solitary crystals* (Fig. 48, C), each occupying the greater part of the cell-contents, are very common, but more frequent are radiating clusters, or rosettes, of crystals (Fig. 48, A). Another widespread type takes the form of bundles of needle-shaped crystals (*raphides*), generally situated in enlarged cells containing mucilage (Fig. 48, B). This last type is particularly characteristic of the Monocotyledons, though by no means lacking in Dicotyledons (*e.g.* Enchanter's Nightshade). In the Solanaceæ, the oxalate of lime is deposited in the form of a powder-like mass of numerous very minute crystals (so-called *crystal-sand*).

Crystals of calcium oxalate are, if present, always found in quantity where active metabolism is going on. In old stalks of Rhubarb a gritty texture is produced by their abundance. They are often very plentiful in the tissues adjoining actively secreting organs (cf. p. 92); also in the leaves of deciduous plants, just prior to leaf-fall, features which respectively emphasise that this substance is a by-product, and that it is not generally useful to the organism.

[1] For reference-books, see p. 97.

The crystals of calcium oxalate are not soluble in acetic acid, but readily dissolve in sulphuric acid, with the production of calcium sulphate. The latter, being itself insoluble, becomes deposited promiscuously in the form of needle-like crystals. These tests serve to verify the presence of oxalate of lime, but usually their application is unnecessary, since crystals of other compounds are very rare.

Many by-products occur in solution in the cell-sap, and of

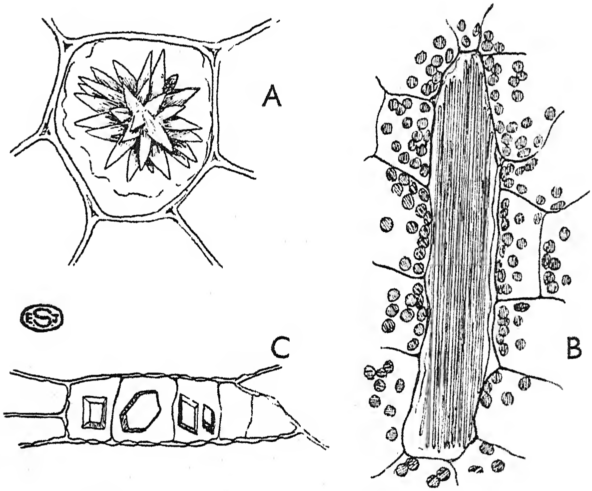

FIG. 48. Crystals. A, Cluster crystals from leaf of Dog's Mercury (*Mercurialis*). B, Raphides from leaf of Enchanter's Nightshade (*Circæa*). C, Solitary crystals from phloem of Horse Chestnut (*Æsculus*).

these the commonest are diverse *organic acids* and bodies known as tannins. The former are responsible for the frequently acid reaction of the sap, and are especially abundant in unripe fruits. As examples mention may be made of malic acid (in Apples), citric acid (in Lemons), tartaric acid (in Grapes), etc. The name of *tannins* is given to diverse organic substances, whose chemical constitution is not fully established, but all of which possess an astringent taste and are characterised by the following reactions: They reduce Fehling's solution, are precipitated by the salts of many metals (*e.g.* basic lead acetate), and take on a blue-black or greenish colour with ferric chloride. Dilute iodine solution, together with a little 10 per cent. ammonia, gives a brilliant red colour even with small quantities of tannins, whilst they are readily precipitated by dilute solutions of caffeine (cf. p. 48).

Tannins are particularly common in the bark of trees (*e.g.* Oak,

Mangrove), in unripe fruits (*e.g.* Pear, Acorn), in leaves (*e.g.* Bracken), and occur abundantly in certain abnormal growths (*e.g.* Oak-galls). They are often accompanied by a yellow or reddish pigment which facilitates recognition of the cells in which they occur. The bark of certain trees (*e.g.* Oak), owing to the large quantity of tannin present, has long been employed in the conversion of hide into leather, which process depends on the coagulation, by the tannin, of the protein substances contained in the animal skin. The reactions of tannins with ferric salts have been extensively used in the preparation of ink.

Another group of by-products, encountered particularly in certain families of Flowering Plants (*e.g.* Ranunculaceæ, Scrophulariaceæ, Solanaceæ, Umbelliferæ), are the *alkaloids*. These are complex basic organic compounds containing nitrogen, which are either dissolved in the cell-sap or present in the solid state; in the plant they are often combined with organic acids. The alkaloids are of such importance, owing to their poisonous and medicinal properties,[1] that the following list of some of the more familiar is given:

Alkaloid.	Action.	Source, etc.
Aconitine .	. Poisonous (used as an antipyretic).	Leaves, root, etc., of Monkshood (*Aconitum napellus*).
Atropine .	. Poisonous (various medicinal uses).	All organs of Deadly Nightshade (*Atropa belladonna*), seeds especially of Thornapple (*Datura stramonium*, Fig. 49) (Solanaceæ).
Cephaeline	. Emetic (active principle of ipecacuanha).	Root of *Psychotria ipecacuanha* (Fam. Rubiaceæ, Brazil).
Cocaine .	. Local anæsthetic.	Leaves of *Erythroxylon coca* (Fam. Linaceæ, Bolivia and Peru).
Coniine .	. Poisonous (paralytic effect).	Seeds of Hemlock (*Conium maculatum*, Umbelliferæ).
Hyoscyne .	. Poisonous (sedative).	Henbane (*Hyoscyamus niger*), *Atropa belladonna*, *Datura stramonium* (Fig. 26).
Morphine	. Narcotic (active principle of opium).	Young fruits of Opium Poppy (*Papaver somniferum*).
Nicotine .	. Poisonous.	Leaves of Tobacco (*Nicotiana tabacum*, Solanaceæ).
Quinine .	. Febrifuge.	Bark of *Cinchona* spp. (Rubiaceæ).
Strychnine	. Poisonous, heart and respiratory stimulant.	Seeds of *Strychnos nux-vomica* (Fam. Loganiaceæ).

The alkaloids as a whole are not characterised by any very specific reactions, but they are precipitated from solution by many different reagents (*e.g.* iodine in potassium iodide, tannic acid). They give very marked colour-reactions with various substances; thus a section of the rhizome of the Monkshood

[1] For further details of the economic importance of these and other substances mentioned in this chapter, see the works cited on p. 67.

treated with a little 50 per cent. sulphuric acid shows a bright red colouration in the parenchyma adjoining the vascular strands, as a result of the presence of aconitine.

The *ptomaines*, which are basic in character, are compounds produced during the decomposition of flesh, etc., by the agency of Moulds and Bacteria, but the effects of so-called "ptomaine-poisoning" are usually due to bacterial toxins. Such stimulants as the caffeine of tea-leaves, coffee-beans, cocoa-beans, and Kola (*Cola acuminata*), and the theobromine present in the Cocoa, are derivatives of purine and very similar to the alkaloids.

FIG. 49. Photograph of part of the shoot, including two fruits, of the Thorn-apple (*Datura stramonium*), which contains the alkaloids atropine and hyoscyne. [Photo. E. J. S.]

The characteristic and often pleasing odour of many Labiatæ (*e.g.* Lavender, Mint, etc.) and Umbelliferæ (*e.g.* Fennel, *Fœniculum*), as well as of flowers, is due to the presence of so-called *volatile* or *ethereal oils*, which are composed of mixtures of hydrocarbons (*i.e.* compounds containing carbon and hydrogen only), known as terpenes, and of their oxygen derivatives. Examples are: lavender oil from the flowers of the Lavender (*Lavendula*); peppermint oil, which contains the antiseptic menthol, from the Peppermint (*Mentha piperita*); bergamot oil, used in the manufacture of Eau de Cologne and other perfumes, from the Bergamot Orange (*Citrus aurantium* var. *bergamia*), a variety of the ordinary Orange;

oil of aniseed from the Aniseed (*Pimpinella anisum*); and the numerous oils from the many species of *Eucalyptus* (Myrtaceæ).

Many of these are used commercially in the preparation of perfumes. Similar oils are the essential principles of such spices as Cloves (*Eugenia caryophyllata*), Cinnamon (the bark of young twigs of *Cinnamomum zeylanicum*), Ginger (the rhizome of *Zingiber officinale*), Pepper (the berries of *Piper nigrum*), etc. Moreover, the active principle of the Hop (*Humulus lupulus*), which is contained in special hairs (cf. p. 161) borne on the bracts of the female catkins, and that causing the odour of Tea, likewise belong to the ethereal oils.

Camphor is a solid terpene-derivative obtained from the wood of the Camphor-tree (*Cinnamomum camphora*), whilst turpentine is a mixture of terpenes which flows from the resin-passages (cf. p. 411) in the trunks of various species of Pines (especially *Pinus pinaster*) and of the Spruce Fir (*Picea excelsa*), when cuts are made in the surface. After the oil of turpentine has been distilled off, the solid residue left is rosin.

Most of the terpenes are colourless, highly refractive liquids, which evaporate completely if sections containing them are heated on a slide for about ten minutes. They are readily soluble in alcohol, chloral hydrate, glacial acetic acid, etc. The ethereal oils are sometimes combined with glucose, etc., in the form of glucosides (*e.g.* the mustard oil of Cruciferæ, cf. p. 79), and become liberated only after coming in contact with the appropriate enzyme.

Flowers owe their colour to pigments, commonly *anthocyanins*, dissolved in the cell-sap of the petals, the colour depending on the nature of the pigment, the reaction of the sap, etc. Such pigments are also frequently present in the vegetative organs, as, for instance, in the Beetroot and in the leaves of *Saxifraga sarmentosa*. Their development appears to be stimulated by excessive transpiration and intense illumination, conditions which are realised in alpine and arctic regions where high colouration is a conspicuous feature.

The yellow and red colouration of many flowers (*e.g.* Garden Nasturtium) and fruits (*e.g.* Tomato) is, however, not due to substances in the cell-sap, but to the presence of pigments (carotin, etc.) in special plastids, termed *chromoplasts*. The pigment often occurs in the latter in a crystalline form. Carotin is present in considerable quantity in the root of the Carrot, to which it imparts the orange colour.

A considerable number of plants are still used as the source of dyes; thus the dried stigmata of *Crocus sativus* yield saffron, and the rhizome of *Curcuma longa* (tropical Asia) the yellow dye turmeric.

It is doubtful whether any of the substances considered are produced for their intrinsic utility to the plant. But it is quite possible that the poisonous alkaloids, the astringent tannins, or the pungent resins may render the plants containing them distasteful to herbivorous animals, and so prove indirectly beneficial. Similarly the antiseptic character of resin may well be of service in

protecting a wound over which it has congealed. The common occurrence of ethereal oils in plants of dry situations has been regarded as bringing about a retardation of transpiration in sunshine. It may be, however, that some of the substances here referred to constitute a means of storage of food-material, and this applies especially to some of the tannins which seem to have the structure of glucosides.

In many plants by-products like those considered above collect as so-called *secretions*. This term is also applied to the sugary liquid produced by the nectaries of flowers, to the watery exudations appearing at different points on leaves under certain conditions, etc. Secretions are very commonly the result of the activity of specialised cells or groups of cells, which may be classed under the general heading of *secretory organs* or *glands*. Their products may pass direct to the exterior, or may be retained in special cavities or canals within the body of the plant. Many of the secretory organs are superficial, and some of these are developed as hairs (cf. p. 160).

Secretions of the nature of ethereal oils, resins, etc., are frequently lodged within the body of the plant. When they are found in isolated cells (*secretory cells*; *e.g.* Bay Laurel, *Laurus nobilis*), the latter often differ, apart from their contents, in shape and in their larger size from the cells of the surrounding parenchymatous tissues. Typical instances are furnished by the so-called tannin-sacs, which are generally characterised by a slightly elongated form; extreme examples are found in the cortex and pith of the Elder (*Sambucus*).

More striking are the *secretory cavities*, *i.e.* large intercellular spaces, approximately isodiametric in form, and again usually lodged in parenchymatous tissues. Often such appear as transparent dots when leaves containing them are held up to the light, a phenomenon well seen in the St. John's Wort (*Hypericum perforatum*) and in the Rue (*Ruta graveolens*). The cavities are filled with an oily secretion, to which these plants owe their peculiar odour. In cross-sections of the leaves of the St. John's Wort the cavities appear more or less circular, each being lined with a layer of thin-walled, somewhat flattened cells (the *epithelium*, cf. Fig. 50, B, *S.*), which discharge the secretion into the central space. The cavities of this plant originate by a gradual separation of the cells, a type of development spoken of as *schizogenous*, and recognisable even at maturity by the presence of a well-defined epithelium; similar schizogenous cavities are encountered in the leaves of the Myrtle (*Myrtus communis*).

In those of the Rue, on the other hand, the cavities arise by a disorganisation of the secreting cells whose remains (cf. Fig. 50, A) persist at the periphery, this mode of origin being described as *lysigenous*; thus at maturity no epithelial layer is present. Similar lysigenous cavities are encountered in the flower-buds known as Cloves (*Eugenia caryophyllata*, Fig. 50, A) and in the skin of the Orange. The secretory cavities of the Rue immediately adjoin the upper epidermis of the leaf, and the secretion in this instance

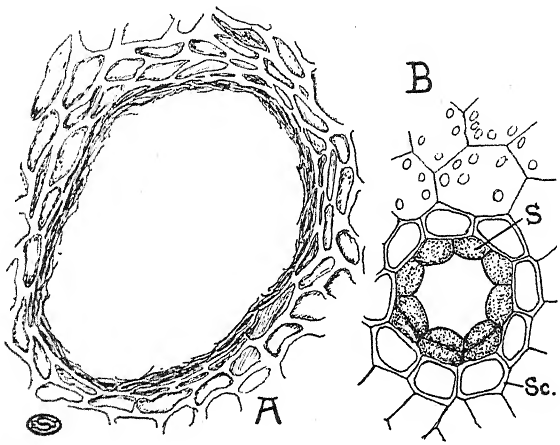

FIG. 50. Secretory organs. A, Lysigenous secretory cavity of the Clove (*Eugenia caryophyllata*). B, Schizogenous secretory canal of the Ivy (*Hedera helix*) in transverse section. *S.*, secretory epithelium; *Sc.*, sclerenchyma sheath.

gradually escapes to the exterior through a zigzagged slit surrounded by four cells; bending of the leaves (*e.g.* by the wind) leads to momentary distortion of the secretory space and consequent emission of part of the secretion. In the Mallows (*Malva* spp.) many parts of the plant contain irregular lysigenous cavities due to the confluence of cells with mucilaginous walls.

In many plants, and especially in the stems and roots, the secretions are present in elongated structures, the *secretory canals*, which are generally schizogenous in origin, the bounding epithelium being developed throughout their entire length. In cross-sections these canals appear as rounded (Fig. 50, B) or oval cavities, whilst in longitudinal sections they are seen to be extensive sinuous tubes which frequently branch and fuse, thus forming a system often pervading all the parenchymatous tissues. The secretory canals are commonly (*e.g.* leaf of the Scots Fir, *Pinus sylvestris*; petiole of the Ivy) enveloped by a sheath of thick-walled cells (Fig. 50, B, *Sc.*),

which prevents compression or collapse through turgor of the surrounding tissue. They often occur in the immediate neighbourhood of the phloem of the vascular bundles, as in the Ivy (*Hedera helix*) and the Umbelliferæ. In the St. John's Wort and certain other plants the secretory cavities of the leaf are replaced by canals in the stem, but the difference is one of shape, not of kind.

It is a familiar fact that in some plants a milky, though sometimes coloured, juice (brilliant orange in the Greater Celandine, *Chelidonium majus*) issues from every cut or broken surface. This latex is especially found amongst British plants in members of the Poppy family (Papavaraceæ), Spurge family (Euphorbiaceæ), Harebell family (Campanulaceæ), a tribe of Compositæ, and in the White Convolvulus (*Convolvulus sepium*); but it is still more characteristic of certain tropical genera. The latex is contained in much elongated tubes which constitute a branched system throughout the thin-walled tissues of the plant and which conform to one of two types.

In the Spurges (*Euphorbia*) the laticiferous tubes can be recognised already in the embryo as several isolated cells, situated just outside the rudimentary vascular system of the cotyledonary node. Each of these *laticiferous cells* elongates considerably as the seedling develops, insinuating itself between the surrounding parenchymatous cells, and this process of growth continues throughout the life of the plant. Thus, even in the adult condition, the number of laticiferous cells remains the same as in the embryo. In the course of their elongation the laticiferous cells develop frequent branches which follow a more or less longitudinal course into all the organs, including the different parts of the flower, but the branches do not fuse with one another. In spite of this extensive growth, which leads to the penetration of the latex-tubes even into the ultimate branches—in tropical Spurges as much as 50 feet above the ground—no cross-walls arise in these elements. On the other hand, as elongation and branching occur, repeated nuclear division takes place, the numerous minute nuclei in the adult laticiferous cell being embedded in the lining layer of cytoplasm which envelops a continuous vacuole occupied by the latex.

In transverse sections through the mature stem of a Spurge, the branches of the laticiferous cells (Fig. 51, *l.*) will be seen at the outer limit of the phloem (*ph.*) as a number of large circular elements with thick white walls. Longitudinal sections, cut tangentially to the phloem, show the characteristic form of the tubes, and branching can often be recognised (Fig. 51, B). The granular latex, which has been coagulated by the preservative (spirit), contains curious starch-grains somewhat resembling minute knuckle-bones.

These, and the thick walls of the tubes, are peculiar to the Spurges, but in other respects the features just described are applicable to all laticiferous cells.

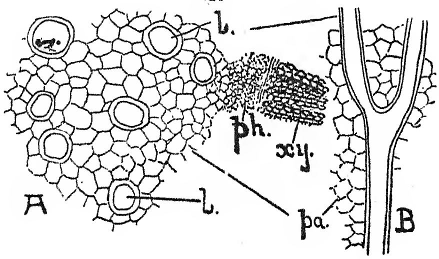

FIG. 51. Laticiferous cells (*l.*) in the stem of a Spurge (*Euphorbia*), in transverse (A) and longitudinal (B) sections. *pa.*, parenchyma of cortex; *ph.*, secondary phloem; *xy.*, secondary xylem.

By contrast *laticiferous vessels*, which are characteristic of Papaveraceæ, Campanulaceæ, and Compositæ, are formed from rows of cells (which may run in any direction, though prevalently longitudinal) by the partial, or usually complete, breaking down of the cross-walls. Laticiferous vessels are usually not recognisable in the embryo, but arise at a later stage in development. They too form an extensive system in all parts of the plant, most commonly near or within the phloem. They are readily distinguished from the laticiferous cells, however, by the occurrence of frequent fusions between their branches, as a result of which they form a highly irregular network (Fig. 52, C). The mode of origin of these elements can seldom be recognised in the adult condition, but in *Chelidonium majus* longitudinal sections show quite clearly remains of the partially absorbed transverse septa.

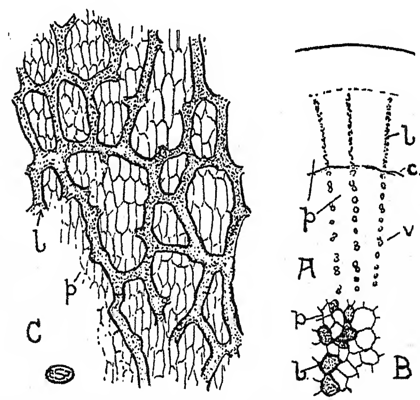

FIG. 52. Laticiferous vessels in the root of the Salsify (*Tragopogon*). A, Diagrammatic representation of a small part of a transverse section, showing the distribution of the laticiferous vessels (*l.*), in relation to the cambium (*c.*), and the vessels of the xylem (*V.*). B, a small part of the secondary phloem enlarged. C, Longitudinal section. *p.*, parenchyma.

Laticiferous vessels are abundant in the fleshy roots of the Dandelion (*Taraxacum*) or Salsify (*Tragopogon*, Fig. 52, A); in transverse sections of preserved material they are plainly recognisable by their brown contents. They have comparatively thin walls and present a very irregular shape (Fig. 52, B, *l.*), which is due to the plane of section often more or less coinciding with that of a

cross-connection between the vertical components of the system; moreover, owing to the thin walls of the laticiferous vessels, the pressure of the surrounding elements leads to distortion. The dense irregular network resulting from the numerous cross-connections is a very prominent feature in a radial longitudinal section (Fig. 52, C, *l.*).

Latex, like milk, is an emulsion, the fluid basis of which is a solution of diverse substances (mineral salts, sugars, proteins, tannins, etc.). Sometimes it includes an important active principle of the plant; for example, in *Papaver somniferum* the alkaloid morphine. The suspended particles include on the one

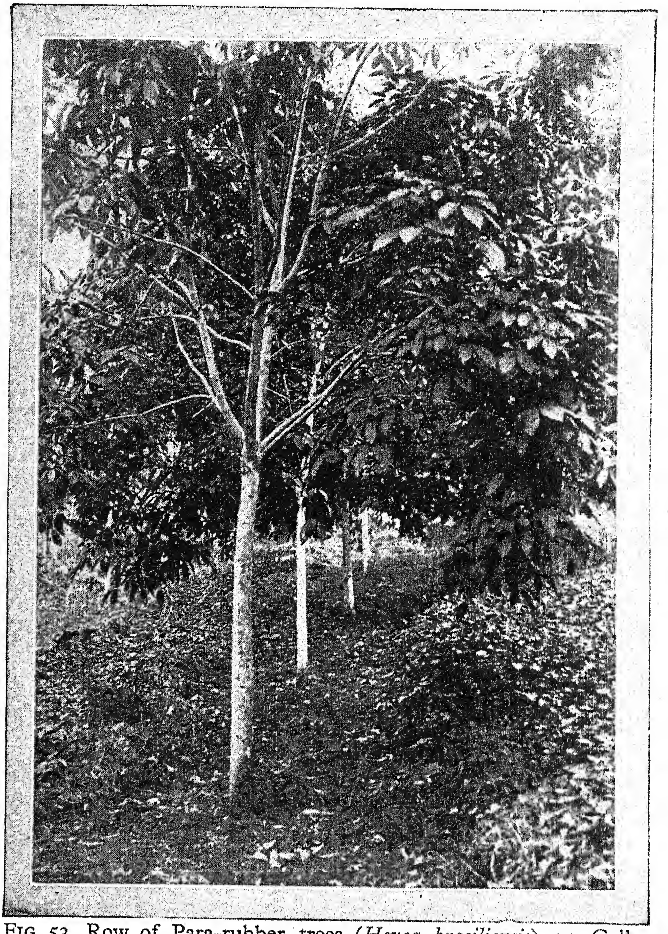

FIG. 53. Row of Para-rubber trees (*Hevea brasiliensis*) on Galley Beach Estates, Ceylon. (Reproduced by permission of the proprietors of the *Indiarubber Journal.*)

hand oil-drops, on the other granules of resin, gum, protein, and caoutchouc, whilst, as already noted, starch-grains occur in the latex of the Spurges. On exposure to air latex as a general rule congeals rapidly, a change often accompanied by discolouration. The latter feature is especially marked in the latex of the Lacquer-tree (*Rhus vernicifera*), where the action is due to an oxidising enzyme (cf. p. 84) which converts the white juice into a dark shining varnish. The "setting" of latex is partly due to evaporation of water, but mainly to a confluence of the oil-globules and suspended particles. The coagulation of the latex, like that of blood, is of advantage in protecting and rapidly covering a wounded surface; moreover, the "dressing" in this case is even antiseptic. The laticiferous elements further serve as food-reservoirs, and in this connection it may be noted that the latex of starved plants becomes thin and watery. Moreover, the frequent association of these elements with the phloem, and the often intimate contact between them and the photosynthetic tissues, seem to indicate a rôle in the storage and transport of elaborated food-material. The by-products, which are not uncommonly present in considerable quantity in the latex, probably render these plants distasteful to animals.

Those plants, whose latex contains a considerable percentage of caoutchouc-particles, are of great economic importance, since they are the source of the *rubber* and *gutta-percha* of commerce. Para-rubber is obtained from a member of the Euphorbiaceæ (*Hevea brasiliensis*, Fig. 53) in which, however, the latex is contained in laticiferous vessels. Other kinds are Ceara-rubber (from *Manihot glaziovii*, Euphorbiaceæ), African rubber (from species of *Landolphia*, family Apocynaceæ), and those obtained from the Indiarubber plant (*Ficus elastica*) and from *Castilloa elastica* (Central America). Gutta-percha is derived from diverse members of a tropical family, the Sapotaceæ, but here the latex is contained in vertical rows of cells.

The latex of rubber trees is obtained by making cuts in the bark and collecting the exuding juice in a small cup. The flow is maintained by paring off thin slices from the lower edges of the cuts, so that the latex-tubes are kept open. After the latex has been artificially coagulated it is washed, and thereupon the raw product is vulcanised. The process of vulcanisation or curing involves a combination of sulphur in varying proportions, according to whether soft rubber or vulcanite is required.

[For further details relating to plant-chemistry, see C. C. Steele, *An Introduction to Plant-Biochemistry*, G. Bell & Sons, 1934 (356 pp.); and P. Haas and T. G. Hill, *An Introduction to the Chemistry of Plant Products*, 2 vols., 2nd edit., Longmans, Green & Co., 1922.]

CHAPTER X

THE ROOT AND ITS FUNCTIONS

THE two chief functions of the root are attachment to the soil and absorption of water, and we may now obtain a further insight into the suitability of the root for these purposes. In the root of a young Bean- or Pea-seedling (Fig. 54) we can distinguish, as in the Shepherd's-purse, root-cap (*r.c.*), root-hairs (*r.h.*), and lateral roots (cf. Fig. 13 of the Bean). The two former are best seen if the seedlings have been kept for two or three days in water.

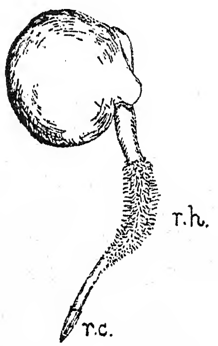

FIG. 54. Young Pea-seedling with radicle showing root-hairs (*r.h.*) and root-cap (*r.c.*) (about twice natural size).

The root-cap serves the purpose of protecting the delicate cells of the meristem at the tip of the root from injury whilst the latter is forcing a passage through the soil. In a longitudinal section the cap is found to consist of a number of concentric layers of thin-walled parenchymatous cells, whose arrangement becomes less regular towards the outside (Fig. 32). During elongation of the root the outermost cells of the root-cap gradually become mucilaginous and break down so that the root-tip glides easily between the particles of soil. The substance of the cap is constantly renewed from the underlying meristem.

There is a varying extent of bare root between the apex and the region occupied by the root-hairs (Fig. 54). It is in this region, and here only, that increase in length is taking place in the new units formed by division of the cells of the meristem (p. 54). To demonstrate this fact we take a number of seedlings having straight radicles (see Appendix X) about an inch long and, using Indian ink, mark off horizontal lines (see Appendix XI) along the root, at intervals of one millimetre from the apex backwards (Fig. 55, A). The seedlings are then attached to a piece of cork

by pins passing through the cotyledons and fixed with the roots pointing vertically downwards in the neck of a jar, the sides of which are lined with wet blotting-paper. The whole is left in a warm dark place for about forty-eight hours.

At the end of this time it will be found that the marks are unequally spaced (Fig. 55, B). Little elongation has taken place, for example, between the lines at the extreme tip, or between those adjacent to the seed. On the other hand, the distance between the fourth and fifth marks has increased very considerably, while the intervals above and below have elongated to a less and less extent until we reach the regions at base and apex where no alteration has taken place. It is thus apparent that growth in length of the root takes place in a very restricted zone, situated a little way behind the apex, and that growth involves the distinct processes of cell-division at the meristem and the subsequent enlargement in the zone of elongation.

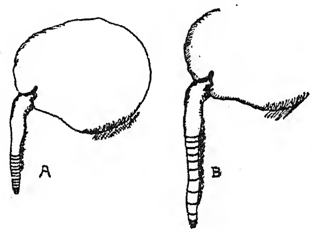

FIG. 55. Experiment to demonstrate region of growth in radicle of Broad Bean (about half the natural size). A, At the beginning of the experiment. B, Forty-eight hours later.

In order to pierce its way through the soil, the growing root must obviously be capable of exerting considerable force. This force is a result of the increase in size of the cells in the zone of elongation and in nature, where the older part of the root is firmly fixed by root-hairs and lateral roots, it serves to drive the apex downwards. Moreover, owing to the restriction of growth in length to a short region, the driving power is exerted close to the apex and therefore the direction of application of the force and the moving tip tend to remain in the same straight line; thus a maximum effect is secured.

The root-hairs arise above the elongating portion of the root, and the advantage of this is clear when it is remembered that their purpose is to absorb water from the soil (p. 7), a function which could not be fulfilled if their position were continually altering with the growth of the root. Moreover, under such conditions the delicate root-hairs would become torn and useless. As it is, however, they develop from that part of the root which has just concluded its growth in length. The root-hairs, which are narrow tube-like outgrowths of the surface-cells (Fig. 116, p. 194), insinuate themselves between the small particles of the soil (Fig. 340, p. 490), with many of which they come into very close contact. It is owing to this that, even after careful washing beneath a tap

of running water, small soil-particles still cling to the finer branches of the roots.

It is, however, not only the front part of the root that is devoid of root-hairs, for the latter usually occupy but a short zone and the hinder part is again bare (Fig. 54). This is because root-hairs are mostly transient structures [1] lasting only a few days, new hairs sprouting out in front as the older ones die away behind. The new hairs arise from surface-cells in which elongation has just ceased and thus, whilst the part occupied by root-hairs always remains at the same distance from the root-apex, the hairs follow the growing tip as it penetrates through the soil. Since root-hairs are developed in exactly the same way on the lateral roots, the growth of the whole root-system carries the region of absorption into an ever-increasing periphery.

The general structure of the root [2] can best be studied in a cross-section through the mature region, the Creeping Buttercup (*Ranunculus repens*) furnishing a suitable example. Under the low power of the microscope the broad parenchymatous *cortex* (Fig. 56, *C.*), whose cells contain numerous starch-grains (*s.*), and the central conducting strand, are sharply contrasted. At the edge of the section is a layer of shrunken cells (Fig. 57, *r.*), some of which are prolonged into shrivelled root-hairs. This epidermis withers above the zone of root-hairs and, since its chief function is their production, it is more usually termed the *piliferous layer*. It is only in sections cut nearer the growing tip that its cells are as yet uncontracted, and can be seen to form a single layer.

The *root-hairs*, each arising from a separate cell (Fig. 57, *r.*), appear as tubular unbranched outgrowths with bluntly rounded tips. The greater part of any root-hair is occupied by a large vacuole continuous with that of the epidermal cell and filled with sap. There is consequently only a thin lining layer of cytoplasm, which is best seen near the tip where the single nucleus usually lies embedded.

Beneath the withered piliferous layer, in the older part of the root, lies the *exodermis* (Fig. 57, *Ex.*), a layer of protective cells

[1] The root-hairs of some plants may persist and function for two or three years.

[2] Important reference-books, dealing with plant-anatomy are: A. De Bary, *Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns* (transl. by F. O. Bower and D. H. Scott), Oxford, 1884 (659 pp.); A. J. Eames and L. H. MacDaniels, *An Introduction to Plant Anatomy*, McGraw Hill Book Co., 1925 (364 pp.); G. Haberlandt, *Physiological Plant Anatomy* (transl. by M. Drummond), Macmillan & Co., 1914 (777 pp.). A comprehensive taxonomic account is given by H. Solereder, *Systematic Anatomy of the Dicotyledons* (transl. by L. A. Boodle and F. E. Fritsch), 2 vols., Clarendon Press, 1908. The companion volume on Monocotyledons is in process of publication in Berlin.

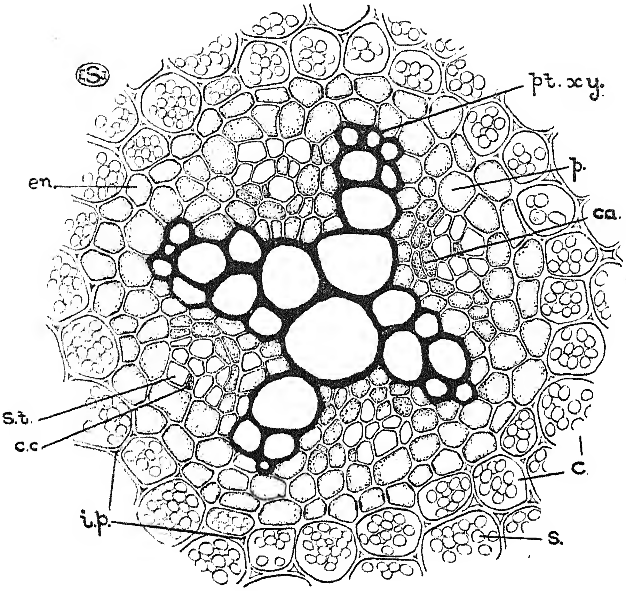

FIG. 56. Transverse section of the central part of the root of the Creeping Buttercup (*Ranunculus repens*). The walls of the xylem elements are shown black. *C.*, inner part of cortex; *ca.*, cambium; *c.c.*, companion cell; *en.*, endodermis; *i.p.*, intercellular spaces; *p.*, pericycle; *pt.xy.*, protoxylem; *s.*, starch; *s.t.*, sieve-tube.

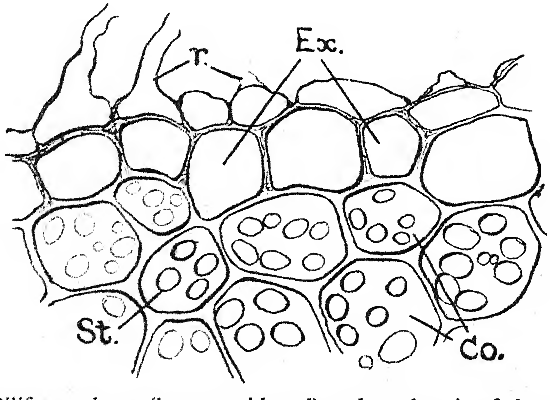

FIG. 57. Piliferous layer (in part withered) and exodermis of the root of the Creeping Buttercup (*Ranunculus repens*). *Co.*, cortex; *Ex.*, exodermis; *r.*, root-hairs arising from cells of piliferous layer; *St.*, starch.

which are on the whole rather smaller than the adjacent cells of the cortex. Their brownish, slightly thickened walls are chemically changed (*i.e.* suberised, cf. p. 186) in such a way that they are almost impermeable to water; but this alteration does not usually take place till the root-hairs begin to wither, so that the water they absorb can readily pass inwards to the vascular cylinder. Sometimes, however (*e.g.* most Monocotyledons), where the exodermis differentiates at an early stage, thin-walled passage-cells (Fig. 64, *P.*), through which the water travels, occur at regular intervals.

The cell-walls of the *cortex* become thinner towards the centre, and intercellular spaces (Fig. 56, *i.p.*) are abundant. The latter form a continuous system which permits of gaseous exchange with the aerial parts of the plant. The vascular strand is delimited from the cortex by two well-defined layers of cells, an outer, the endodermis (*en.*), and an inner, the pericycle (*p.*) (cf. below).

In sections stained with aniline chloride a four-rayed group of yellow elements, composing the lignified wood or *xylem* (Fig. 56), occupies the greater part of the conducting strand. In the bays between the four arms of the xylem are oval groups of small-celled unstained tissue, the *phloem*, in which the wide and empty-looking sieve-tubes (*s.t.*) are plainly distinguished from the narrower companion-cells (*c.c.*) with their dense contents (cf. p. 62). Each phloem-group is separated from the adjacent xylem by one or two layers of parenchyma (*ca.*).

The xylem consists chiefly of dead, empty-looking elements, the vessels, of which those at the centre of the conducting strand are the largest, whilst the remainder become progressively smaller in passing outwards along any one of the rays. The end of each xylem-arm, immediately beneath the pericycle, is thus occupied, by a strand of the narrowest vessels (Fig. 56, *pt.xy.*). In cross-sections, through younger parts of the root, a larger or smaller number of the central vessels will appear thin-walled and unlignified, showing that differentiation of the xylem takes place from without inwards. The small peripheral elements are the *protoxylem*, and the larger later-formed ones are termed the *metaxylem*.

Longitudinal sections passing through one of the xylem-arms will show that the vessels of the protoxylem are spirally thickened, whilst those of the metaxylem bear bordered pits. The walls between the larger vessels, in the transverse section, exhibit a thin dark line down the middle (the middle lamella), with the thickening layers on either side. These latter are not homogeneous, however, but appear to consist of short dark lengths alternating with lighter and narrower portions, where the pits are seen in optical section.

The cells of the *endodermis* (Fig. 56, *en.*) are distinctly smaller than the adjacent cortical cells and somewhat flattened. Their radial walls are thicker and look darker than the others, although when sharply focussed in optical section they appear bright owing to their highly refractive character. On treatment of a section with strong sulphuric acid, the membrane swells and dissolves, except for the radial walls, which persist unaltered, implying that they are chemically different from the other walls of the endodermal cells. These features of the radial walls are commonly exhibited by the endodermis of roots, and a layer with similar thickenings is found in the stems of aquatics (cf. p. 544). This thickening extends all round each endodermal cell so that the vertical and horizontal walls form an impervious network, the meshes of which are occupied by the protoplasts.

The purpose of the endodermis is still obscure. The firm lateral connection of the cells due to the thickening renders this layer an efficient sheath to the vascular system. The considerable thickening of the entire endodermal wall, which obtains in some roots (cf. below), suggests a probable mechanical value. In the unthickened state this layer may serve to cut off the water-conducting strand from the air-spaces of the cortex, a delimitation rendered necessary by the frequent differences in pressure (due either to root-pressure or negative pressure, pp. 194, 203) on its two sides. Moreover, all liquids must necessarily pass through the protoplasts of the endodermal cells. Not uncommonly the layer of cortical cells next to the endodermis develops characteristic thickenings on the transverse and radial walls, a feature well seen in the roots of many Cruciferæ (*e.g.* White Mustard), and no doubt of mechanical value.

The *pericycle* which lies immediately within the endodermis is another continuous layer not characterised by any structural peculiarities (Fig. 56, *p.*).

Many of the features just described are typical of roots generally, viz. the aggregation of the vascular tissue near the centre; the alternation of phloem and xylem resulting in a radial structure; the peripheral location of the protoxylem; the wide cortex; the presence of an endodermis with its special differentiation; also the occurrence of exodermis and piliferous layer. Roots differ among one another in two principal respects—namely, as to the number of phloem- and xylem-strands, and in the presence or absence of parenchyma (pith) in the centre of the conducting tissue. As regards the former feature, there may be two or more of such strands, roots being described as *diarch*, *triarch*, *tetrarch* (Fig. 56), *pentarch* (Fig. 59), etc., according as the number of alternating

xylem- and phloem-groups is two, three, four, or five, etc., whilst when they are numerous the structure is said to be *polyarch* (Fig. 58). Thus the root just examined is tetrarch, that of the Wallflower diarch, and that of most Monocotyledons polyarch. A *pith* composed of parenchyma, which is sometimes thick-walled, is frequent in the roots of herbaceous Dicotyledons (Fig. 59) and

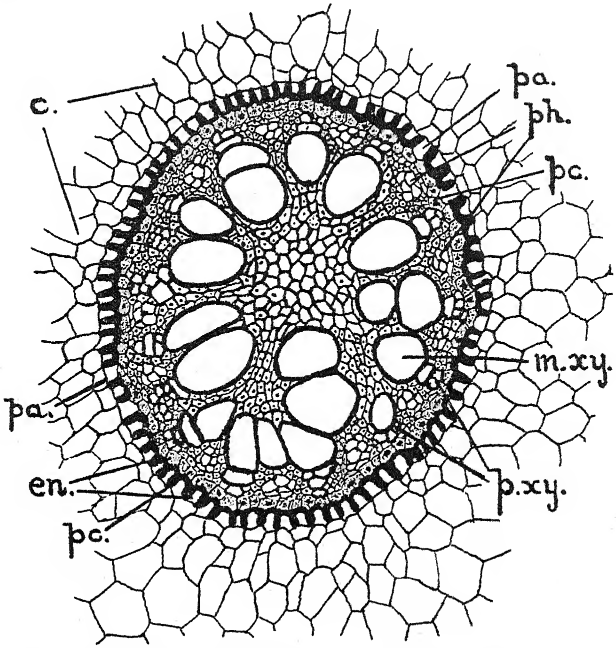

FIG. 58. Transverse section of the central part of the root of *Iris*. *C.*, cortex; *en.*, endodermis; *m.xy.*, metaxylem; *pa.*, passage cells; *pc.*, pericycle; *ph.*, phloem; *p.xy.*, protoxylem.

in Monocotyledons (Fig. 58), but in woody Dicotyledons and Conifers the xylem-groups often meet at the centre. Roots also vary in the manner of thickening of the mature cells of the endodermis and the number of layers constituting the pericycle.

A transverse section of the root of the *Iris* illustrates these features. It exhibits the typical Monocotyledonous structure, viz. a central pith and numerous alternating groups of xylem and phloem (Fig. 58). The endodermis (*en.*) is conspicuous owing to the marked thickening of all but the outer walls of most of its cells. Opposite the protoxylem groups (*p.xy.*), however, the endodermal cells are often thin-walled, and such *passage-cells* (*pa.*) serve for the transference of water through the endodermis, which

is elsewhere impermeable. A thickened endodermis interrupted by thin-walled passage-cells is found particularly amongst Monocotyledons (see also Fig. 64, *Pa.*).

The side-roots arise at some considerable distance from the tip of the main root (Fig. 12, C; Fig. 15, E), and careful observation shows that they have burst through the outer covering of the latter (Fig. 59). The mode of origin of the laterals can be readily

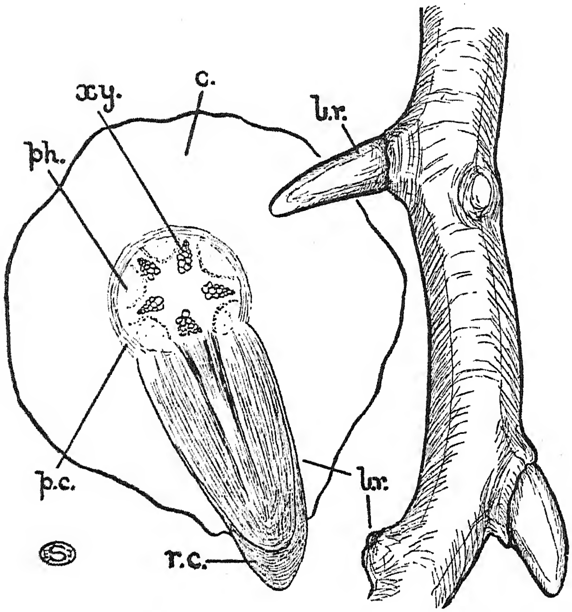

FIG. 59. The root of a Bean seedling in surface-view and in transverse section showing the origin of the lateral roots (*l.r.*). *C.*, cortex; *ph.*, phloem; *p.c.*, pericycle; *r.c.*, root-cap; *xy.*, xylem.

studied in longitudinal sections through a Bean root. The lateral roots arise by division of pericycle cells, either opposite the protoxylem strands (Fig. 59, *l.r.*), or between these and the phloem, so that in Dicotyledons they form vertical series equal to or double the number of xylem groups. In Monocotyledons, owing to the numerous protoxylem-strands, and the early decay of the tap-root, this arrangement is often obscured.

A short distance behind the apex young laterals, which have not yet reached the surface, are distinguishable. In the course of their further development, the side-roots push their way through the cortex, so that, by the time they emerge at the surface, the protective root-cap is fully formed (Fig. 59, *r.c.*). This so-called

endogenous origin contrasts with the superficial origin of the branches of the stem, and can be related to a need for protection, until the young root has developed sufficiently to withstand the resistance of the soil.

All, even the finest members of a root-system, show an identical structure, and the principal difference between the main root and its branches lies in their direction of growth. The factors causing the downward growth of the main root can be investigated by the following experiments.

A number of healthy seedlings having straight radicles (Appendix X) are pinned parallel to one another to the surface of a large cork; the latter is then fixed edge on to the bottom of a light-tight box in such a way that the radicles are horizontal and free to bend. The entire inner surface (including the lid) is lined with wet blotting-paper, and the whole is left in a warm place for about twenty-four hours. The tips will then be found to have curved downwards into a vertical position. It is plain that the roots were subjected equally on all sides to moisture, warmth, supply of air, and darkness, and the only one-sided influence is the force of gravity. The root then, unlike the shoot of most plants (cf. p. 15), grows in the direction of this force and is thus led to penetrate deeper and deeper into the soil. On the other hand, light which plays an important part in determining the direction of growth of the shoot, has little influence on the roots of most plants.

Examination of the root-system of such plants as the Shepherd's-purse and the Pea discloses the fact that the laterals diverge at more or less of an acute angle from the main root, so that they grow outwards and downwards (Figs. 2, 12, 15). In order to observe readily the growth of the root-system we can employ a rectangular wooden box, provided with drainage-holes as described on p. 35; one long side of the box is replaced by a sheet of glass which slopes *inwards* from the top at a slight angle. The box is filled with soil and seeds are planted at the surface in close contact with the glass, the whole being placed in darkness. Owing to the downward tendency of the root-system the main root and its laterals remain in close touch with the glass surface. The box is propped up so that its floor is at an angle of 45° with the ground, and the experiment left for about three days. It is then observed that the tip of the main root, as in the preceding experiment, has curved down into the vertical position; the tips of the laterals have also curved, so that these tips now lie at the same angle as before with the new direction assumed by the growing part of the main root—a fact which can be verified by measuring the old and

new angles with a protractor. The direction of growth of the laterals is thus also influenced by gravity, but forms a constant angle with that of the main root.

Arising from the laterals of the first order are smaller roots of the second order, and in a strongly developed root-system there may even be branches of a higher order (Fig. 2). These ultimate members of the root are unaffected by gravity and generally extend into the soil in all directions. Hence the volume of soil occupied by the root-system is very completely exploited by its numerous ramifications.

Apart from gravity, there is, however, one other condition that markedly influences the direction of growth, especially of the finer branches of the root-system, and that is the distribution of moisture. To demonstrate this fact we use the same box as in the last experiment with the following modification (Fig. 60): A small clean

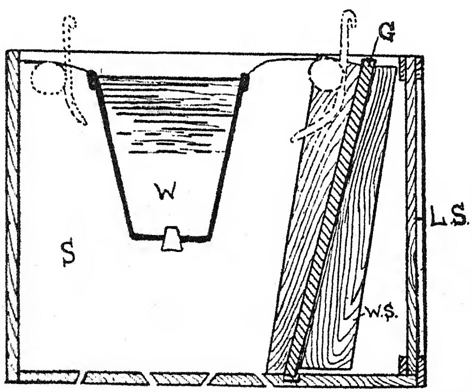

FIG. 60. Experiment to demonstrate hydrotropism in roots. The box is shown in section; the final appearance of two seedlings is indicated by dotted lines. *S*, soil; *W*, water in central pot; *G*, sloping glass front of box; *L.S.*, light-shield. *W.S.*, wooden supports for glass front.

flower-pot, the hole at the base of which is firmly plugged to prevent leakage, is filled with water and embedded up to its rim in the soil which otherwise fills the box and which should be moderately dry. Soaked seeds (*e.g.* Pea, Bean) are planted against the glass as before, but some are also placed in the surface layer of the soil in other parts of the box. Water is supplied to the soil only by way of the flower-pot which is kept full. After having remained in darkness[1] for about ten days, the roots of the seedlings planted against the glass are scarcely visible and, on uprooting them carefully, it will be seen that this is due to their having curved more or less markedly towards

[1] This can be effected by means of a wooden light-shield, shown in Fig. 60.

the pot which is the only source of moisture in the soil (see Fig. 60). Moreover, the seedlings which have developed from the seeds planted elsewhere in the box will, if carefully uprooted, also show a marked curvature of their roots towards the pot. The success of the experiment depends on the realisation of a correct moisture gradient. The influence of unequal distribution of moisture on the direction of growth of roots is described as *hydrotropism*.

The type of root-system with which we have hitherto become familiar (*e.g.* in the Shepherd's-purse, Fig. 2) is characterised by the possession of a prominent main root (often spoken of as a *tap-root*) growing vertically down into the soil and bearing numerous branches that become progressively smaller. This type is most commonly found in Dicotyledons. In Monocotyledons, on the other hand, as well as in many Dicotyledons, the root-system consists of a number of members in which we cannot distinguish any single one as specially prominent; such a root-system is described as *fibrous*, and good examples are furnished by the Strawberry (Fig. 139, p. 224), the Hyacinth and Grasses (Fig. 65, C). We have already met with an instance of this kind in considering the germination of the Maize (p. 31).

The radicle, which usually gives rise to the tap-root, in all fibrous root-systems fails to develop to any considerable extent. The tuft of roots originates either by outgrowth from the base of the stem (Grasses, Strawberry, etc.) or from the hypocotyl (Groundsel, Sanicle). Owing to the fact that they do not arise from roots, these laterals are described as *adventitious*. Another good example of such adventitious roots is seen in the Ivy (Fig. 61), where they appear on the side of the stem adjacent to the wall and serve to fix the plant. The propagation of plants by cuttings (*e.g.* Geraniums, Osier-willows) is dependent upon the development of adventitious roots from the part of the stem placed in the soil. In many Willows the rudiments of such roots are already visible as little knob-like swellings beneath the nodes of the uncut stem.

We may now consider how the structure of the root is related to its two principal functions, the absorption of water from the soil and the anchorage of the plant. Absorption of water takes place mainly through those regions in which the piliferous layer is still intact and living. The outgrowth of its cells into root-hairs, the chief organs of absorption, affords an enormously increased surface over which the latter can take place. The size and number of the root-hairs tend to decrease with increasing wetness of the soil, and in some marsh-plants (*e.g.* Marsh Marigold) and a considerable number of aquatics they may be altogether absent. Here, owing to the high water-content of the soil, an enlargement of the absorb-

ing surface confers no benefit as regards water-supply. The root-hairs not only function in absorbing the water with its dissolved mineral salts, but themselves play a part in rendering substances in the soil available (p. 208). The older part of the root which does not appreciably absorb is amply protected by the exodermis.

In plants in which the overground organs persist and form a woody skeleton, the development of this aerial system is accompanied by a similar change in the root. Most trees at first possess a tap-root, but, as the plant becomes older, the laterals near the surface of the soil frequently develop more strongly and form a horizontal platform which serves to support the plant and distributes the pulling strain (due to the action of the wind) over a wider area. Such roots often appear above the surface of the ground as a system radiating from the base of the main trunk, this being due to their own increase in thickness, as well as to removal of soil by rain. The bulk of such a woody root-system no longer serves the purpose of absorption, this function being restricted to its finest branches. It is a familiar fact that the foliage of most trees affords a more or less efficient shelter from rain, the water draining off from the edge of the canopy. Since the roots develop *pari passu* with the crown of foliage, their absorbent branches are thus usually located beneath the drip of the tree.

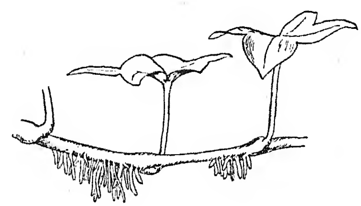

FIG. 61. Portion of a climbing shoot of Ivy (*Hedera helix*), showing the adventitious roots and three nodes (somewhat reduced).

The root is suited to its anchoring function by its more or less extensive branching, and the central location of the mechanical elements which enable it to withstand the pulling strain to which it is subjected. In most roots the mechanical tissue is constituted merely by the xylem, as well as by the pith when the latter is thick-walled, but in the Pea and other Leguminosæ groups of fibres are developed in relation to the phloem. When roots serve not only for anchoring, but also for the support of the plant, a modified structure may obtain.

In the Maize, after the plant has reached a certain height, additional adventitious roots arise from the stem, some little way above the surface of the ground, and grow obliquely downwards into the soil (Fig. 62, C). These *prop-roots* serve the purpose of augmenting the somewhat feeble primary root-system which is insufficient to maintain the tall Maize plant in the erect position. Better examples are furnished by the tropical Mangroves which

grow in loose shifting estuarine mud subjected to tidal inundation.

A cross-section of a *prop-root* of the Maize (Fig. 62, A) contrasts with one of an ordinary root of this plant in the presence of a special cortical ring of mechanical elements and the larger size of the central cylinder, so that the xylem also is more peripheral.

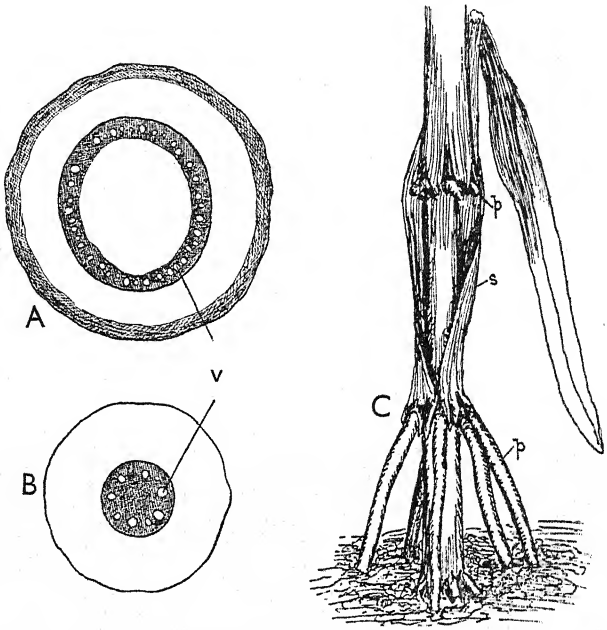

FIG. 62. Diagrams of a normal absorbing root (B) and of a prop-root (A) of the Maize (*Zea mais*). The sclerenchymatous tissues are indicated by shading. *v.*, vessels; *C.*, lower part of plant of Maize, showing prop-roots (*p*) arising from two nodes, the upper ones in an early stage of development (about natural size); *s*, sheath of lowest leaf.

In both these respects the mechanical construction of such a prop-root approaches that of a stem (cf. p. 144).

Many plants characteristic of soils rich in humus exhibit an intimate relation of fungal threads with their roots or other underground organs. In some these threads form a dense weft over the whole surface (*ectotrophic mycorrhiza*, *e.g.* Beech, *Monotropa*, etc.), and appear to replace the absent root-hairs. In others the Fungus can be seen occupying a definite zone *within* the cortex [*endotrophic mycorrhiza*, *e.g.* Bird's Nest Orchid (Fig. 63, *m.*), Heather, etc.]. The advantage of association with the Fungus would appear to depend mainly on the power of the latter to break down and absorb

the organic material which is then in part utilised by the Flowering Plant (cf. p. 218).

Many tropical Orchids which grow high up in the forks of trees possess tufts of roots protruding into the humid air. These *aerial roots* exhibit a modification of structure in correspondence with their special functions as organs of absorption and photo-

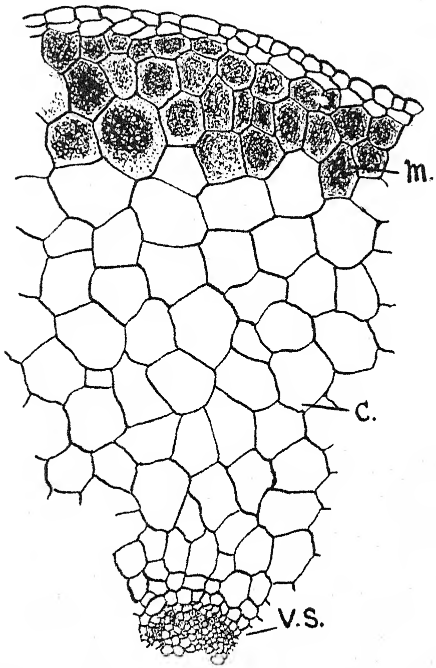

FIG. 63.—Transverse section of the outer part of one of the underground branches of the Bird's Nest Orchid (*Neottia nidus-avis*), showing the vascular strand (*V.S.*), the cortex (*C.*), and the mycorrhizal zone (*m.*).

synthesis. The cortical cells frequently contain chlorophyll, a feature doubtless related to their growth in light, since ordinary terrestrial roots (*e.g.* those of the Pea) will often become green when exposed to illumination. In extreme instances (*e.g. Tænio-phyllum*) the entire photosynthesis is carried out by means of aerial roots, which assume a leaf-like appearance, whilst the true leaves are mere scales. The absorption of water in such roots is accomplished with the aid of a tissue formed by a remarkable development of the epidermis (the *velamen*, Fig. 64, *V.*). The dermatogen usually divides to form several, or many, layers of cells, which ultimately lose their living contents and often exhibit

a spiral or reticulate thickening. Moreover, large holes frequently develop in the walls of many of the cells, as a result of which any moisture falling or condensing on the surface is rapidly absorbed. The exodermis (Fig. 64, *Ex.*), situated at the inner edge of the velamen, is interrupted by thin-walled passage-cells (*P.*) for the

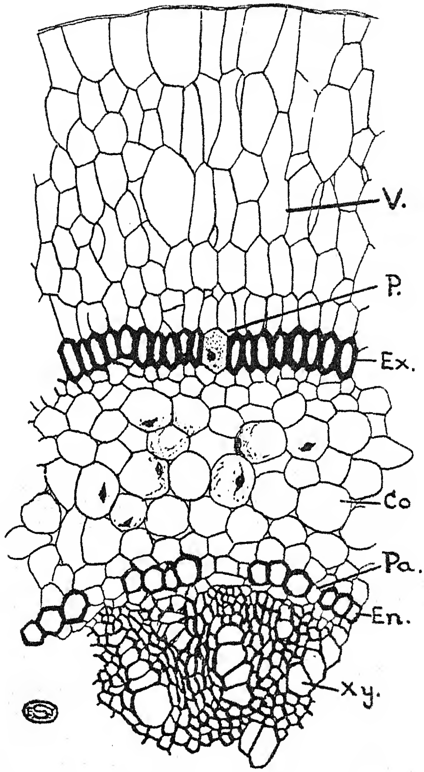

FIG. 64. Transverse section through part of a root of an epiphytic Orchid (*Dendrobium*), showing the velamen (*V.*). *Co.*, cortex; *En.*, endodermis; *Ex.*, exodermis; *P.* and *Pa.*, passage cells; *Xy.*, xylem.

inward transference of the water absorbed. In dry weather air fills the cells of the velamen, so that they appear white and opaque; but when occupied by moisture they become translucent and the green colour of the cells beneath is visible.

In biennials and herbaceous perennials the roots frequently serve as storage-organs for the food-materials, laid up for subsequent growth (see Chapter II), and in consequence become more or less swollen. Frequently it is the tap-root which enlarges in

this way, and good examples are furnished by the Carrot (Fig. 65, A), the Parsnip, and the Dock. The swollen structure in the Turnip (Fig. 65, D) consists largely of a tap-root, but in the formation of the uppermost portion the hypocotyl and the base of the stem appear to participate, since remains of leaves are often

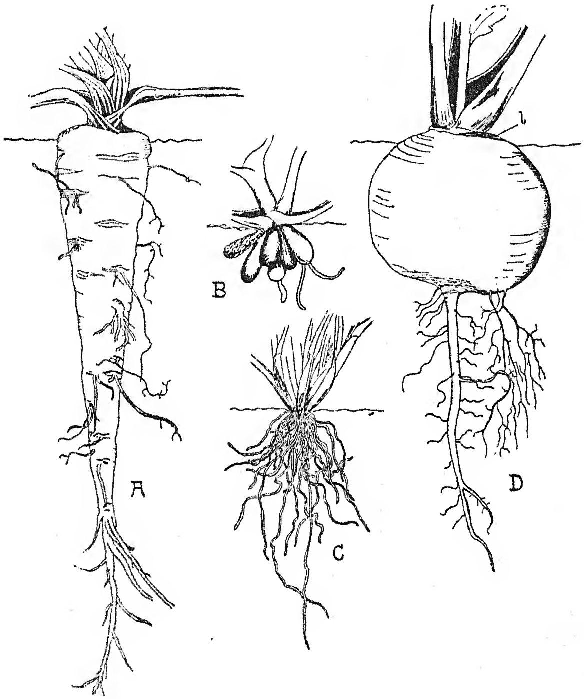

FIG. 65. Different types of root-systems (reduced to about half natural size). A, Carrot. B, Lesser Celandine. C, Grass. D, Turnip. The level of the ground is in all cases shown by a black line. *l*, leaf-scar.

found in this region (Fig. 65, D, *l*). In the Dahlia and Lesser Celandine (*Ficaria verna*, Fig. 65, B), on the other hand, many of the members of the fibrous root-system are swollen, and the enlarged roots are often spoken of as *root-tubers*. The tubers of a Lesser Celandine bear near their tip an axillary bud from which new growth ensues in the following spring. The underground tubers of British Orchids are swollen adventitious roots which arise upon an axillary bud. The examples just given include a number of our common vegetables which owe their utility to the large quantities of food-reserves contained in the storage-organs, and

as further instances we may add the Radish, the Beetroot and the Mangold wurzel (*Beta vulgaris* var.).

The slight variation in the morphology and anatomical construction of roots can be related to the comparatively uniform environment, the soil, in which they develop. Indeed, as we have seen, the only marked departures from the normal structure are associated with special functions.

CHAPTER XI

THE ARCHITECTURE OF THE SHOOT

THE shoot usually grows erect in response to the directive influences of light and gravity (p. 14), though occasionally it may exhibit a prostrate or climbing habit. The shoot differs greatly in appearance from plant to plant. This variety of form is determined by the way in which the stem branches, as well as by the shape and mode of arrangement of the leaves, and to understand the architecture of the shoot these features must be considered separately.

It is easiest to study the mode of branching in the first place on woody plants, because the succession of events is more clearly seen in them than in herbs which frequently do not branch much until the time of flowering. If we examine a woody shoot, as for instance one of the larger branches of the Beech, in winter-time (Fig. 66, A), we find that it is terminated by a long, slender and pointed structure of a brown colour, the *terminal bud* (*t.b.*); this contains in miniature and telescoped together next year's continuation of the branch. Along the sides of the latter are a number of perfectly similar buds (the *lateral buds*, *l.b.*), each capable in the next season of growing out into a side-branch. Beneath each lateral bud the bark shows a smooth scar (*l.s.*), generally well defined and bearing a curved band of dots. Each scar marks the former position of a leaf (*i.e.* it is a *leaf-scar*, see also Fig. 67), and the dots on its surface are the broken ends of the vascular strands joining stem and leaf. The lateral buds, therefore, are all axillary (p. 2) to leaves of past seasons, the terminal buds alone having no subtending leaf-scars. In some plants (*e.g.* some Willows) more than one bud (*accessory buds*) may arise in a leaf-axil, either above or on either side of the usual one (cf. also p. 264).

Other external features of the twigs are the *lenticels* (Fig. 66, A, *l*; Fig. 67), small generally lighter-coloured projections of varying shape, which are irregularly distributed on the bark of woody plants and serve the purpose of gaseous interchange between the interior of the branch and the atmosphere, prevented except at these points by the impermeable bark.

The most fundamental distinction in the mode of branching lies in the behaviour of the terminal bud. In a considerable number of trees, of which the Conifers furnish excellent examples, the original plumule of the seedling steadily continues its growth year by year, lengthening out in the spring and producing a new

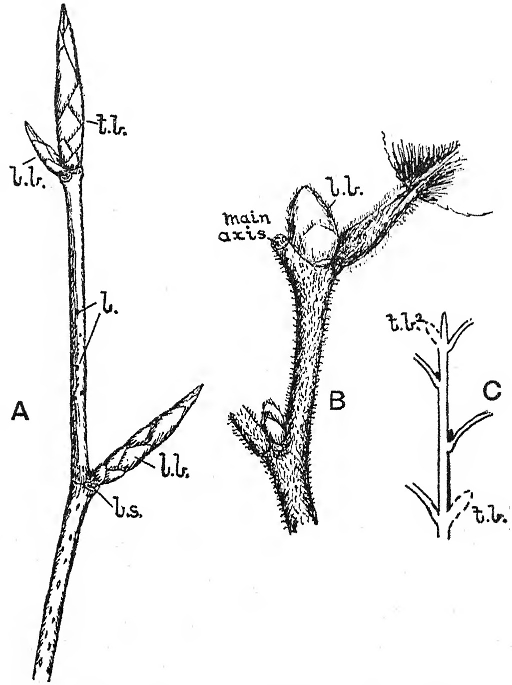

FIG. 66. Winter state of twigs of Beech (A, about natural size) and Elm (B, somewhat enlarged). C, Diagram to explain behaviour of terminal bud in the Elm or Lime. *l.*, lenticels; *l.b.*, lateral buds; *l.s.*, leaf-scar; *t.b.*, terminal bud; *t.b.*[1] and *t.b.*[2] in Fig. C, terminal buds of successive seasons which die away.

terminal bud in the autumn, so that a tall, straight, main axis (or monopodium) is produced. A certain number of lateral buds develop into side-branches of the first order, but these are all subsidiary to the central shaft and again branch in the same manner. Moreover, in this method of *monopodial* branching the oldest and largest laterals are farthest from the growing tip, whilst the youngest and smallest are close to it. As a result of this very regular branching, such plants often exhibit a very symmetrical conical shape, well seen in a good specimen of a Christmas tree.

The most essential characteristic of the type just considered

is the persistence of the meristem of the main axis from year to year, and herein lies the distinction from so-called *sympodial* branching. This latter is seen in its simplest form in the Elm (Fig. 66, B and C) or Lime. If a branch of one of these trees be examined in the course of the summer, it will be found to possess a well-marked terminal bud, but as the season advances this bud

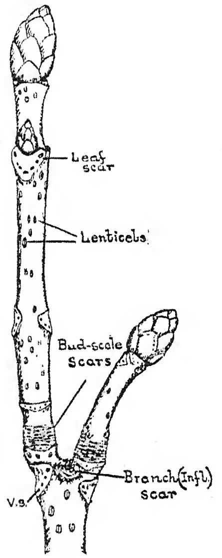

FIG. 67. Portion of twig of Horse Chestnut (*Æsculus*) showing buds, leaf-scars and lenticels (about two-thirds natural size). *v.s.*, vascular strands.

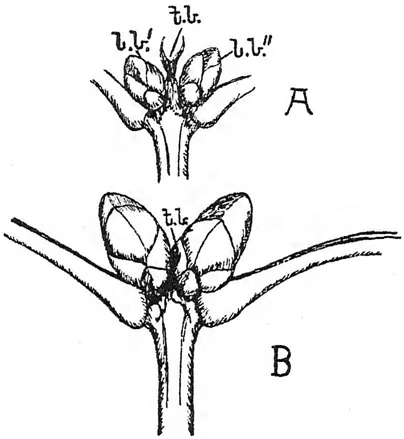

FIG. 68. Twigs of Lilac (*Syringa vulgaris*) illustrating dichasial branching and dying away of terminal bud. A, Young stage, about natural size. B, Older stage, slightly enlarged. *l.b'*, *l.b.''*, lateral buds; *t.b.*, terminal bud.

begins to show signs of withering, while the axillary bud situated just beneath it increases in vigour. Ultimately, when the winter arrives, this axillary bud will be found to occupy a position at the extreme end (Fig. 66, B, *l.b.*), the true terminal bud being represented by a small shrivelled remnant or scar (main axis in Fig. 66, B) at one side. Careful examination even at this time, however, shows that the bud at the end of the branch is not a true terminal one, since beneath it is found a leaf-scar (cf. p. 155).

The lateral buds which thus always come to occupy the ends of the branches in the Elm or Lime continue the growth of the latter in the following season, so that as the years go on there is

built up a composite axis or sympodium, consisting of a succession of lateral branches, so adjusted as to form an apparently continuous whole (cf. Fig. 66, C). In some plants, however, sympodial branching does not take place with complete regularity.

In the Horse Chestnut (Fig. 67), for example, frequent monopodial branching takes place, and sympodial branching occurs only in connection with flowering. The inflorescence (p. 5) of this tree forms the termination of the branch upon which it is borne; when flowering and fruiting are over, the stalk of the inflorescence is shed and leaves a large round somewhat sunken scar (Fig. 67, infl. scar). The nearest lateral bud grows into the line of continuity and in the next season replaces the branch whose further growth terminated with the production of flowers. Circular scars marking the former attachment of inflorescences are always to be found on branches of the Horse Chestnut (Fig. 67).

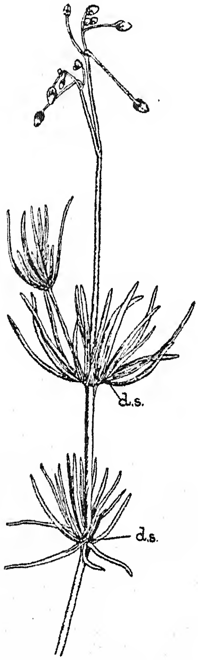

FIG. 69. Branch of the Field Spurrey (*Spergula arvensis*), showing dwarf-shoots (*d.s.*) (about two-thirds natural size).

The Lilac (Fig. 68) shows a slightly different type of sympodial branching. Here the terminal bud usually, though not invariably, either dies, or its existence is terminated by the formation of an inflorescence, as in the Horse Chestnut. The difference, as compared with the previous examples, is that two lateral buds, instead of one, grow out to replace the main axis, so that it looks as if the latter had forked.[1] This so-called *dichasial* branching is also well seen in the Mistletoe and occasionally in the Horse Chestnut.

The extent of branching varies greatly; on the one hand are plants, like most Monocotyledons, in which it is practically restricted to the region of the inflorescence, whilst on the other are richly branching trees, such as the Beech or Elm. In all woody plants, however, the materials available for growth suffice for the development of only a small number of the buds, a very considerable percentage being doomed to inactivity, either permanent or temporary. These inactive or *dormant buds* retain their vitality often throughout the life of the tree or shrub and are ready to grow out into branches, should occasion demand. That lack of nourishment

[1] Cf. Dichotomy, p. 288.

is largely responsible for preventing further development is easily seen if we remove the terminal portion of any given branch; thereby lateral buds borne lower down upon it which would otherwise remain dormant are caused to sprout (cf. p. 249). Upon this depends the principle of hedge-making, in which by cutting off the tops of the upper branches numerous laterals are caused to develop, so that a dense growth results.

In a few plants (*e.g.* Scot's Fir, Field Spurrey, Fig. 69) most of the lateral branches do not elongate in the normal way, but remain quite short owing to the non-development of the internodes; such branches are termed *dwarf-shoots* (Fig. 69, *d.s.*). Most of our fruit-trees exhibit a similar phenomenon, but here a few of the lower internodes are developed, so that these *spur-shoots* do not remain quite as short as typical dwarf-shoots.

In all the above examples we have spoken of shoots as arising from normal buds developed in the axils of leaves. Exceptionally, however, shoots may originate in another way, as, for example, from the cut stumps of trees, from roots (*e.g.* in the Bindweed and Poplar) or from foliage-leaves (*e.g. Cardamine pratensis*). The term *adventitious*, which has already been applied to roots (p. 108), is used also for such shoots, developing in an unusual position.

The majority of plants exhibit but a single leaf at each node, an arrangement described as *alternate*, but there are quite a large number (*e.g.* Lilac, Fig. 68; Hop, Fig. 10; Hedge Woundwort, Fig. 70, C) in which a pair of leaves arise together, when the leaf-arrangement is said to be *opposite*. Such pairs of leaves almost invariably occur at right angles to one another at successive nodes (Fig. 70, C), *i.e.* they are *decussate*. Occasionally, as in the Teasel (*Dipsacus*) and Yellow Centaury (*Chlora*), the bases of the two opposite sessile leaves are joined together so as to surround the stem, a condition described as *connate*. If more than two leaves occur at a node the group is spoken of as a *whorl*, examples being seen in the Oleander (*Nerium*) and the Water Milfoil (*Myriophyllum*, Fig. 388); here again the leaves of one whorl usually alternate with those above and below. A result of such alternation between the leaves of successive nodes is the prevention of undue overshadowing, and the same advantage accrues from the spiral arrangement of alternate leaves (cf. below).

In many herbaceous plants (*e.g.* Dandelion, Shepherd's-purse, Fig. 1) a large number of leaves arise close together from the base of the stem, just above the surface of the soil; such leaves are usually collected in the form of a rosette and are described as *radical* leaves (Fig. 1, *r.l.*), in contrast to those borne on the upper part of the stem, the *cauline* leaves (Fig. 1, *c.l.*).

The simplest possible type of alternate arrangement is for one leaf to be separated by half the circumference of the stem from that at the next node, so that the leaves form two vertical rows. This *distichous* arrangement is well seen in the Hazel (Fig. 70, A), in Grasses and in the Ivy (Fig. 61) and is often expressed simply by the fraction $\frac{1}{2}$. In the Beech and in the Sedges, for instance, the leaves are closer together, forming three vertical rows on the stem and being separated from one another by only one-third of the circumference; the arrangement is therefore *tristichous* and can be briefly represented by the

fraction $\frac{1}{3}$. One of the commonest types is for successive leaves to follow at intervals approximately equal to two-fifths of the stem's circumference (Fig. 70, B).

In plants having a spiral leaf-arrangement the interval between successive

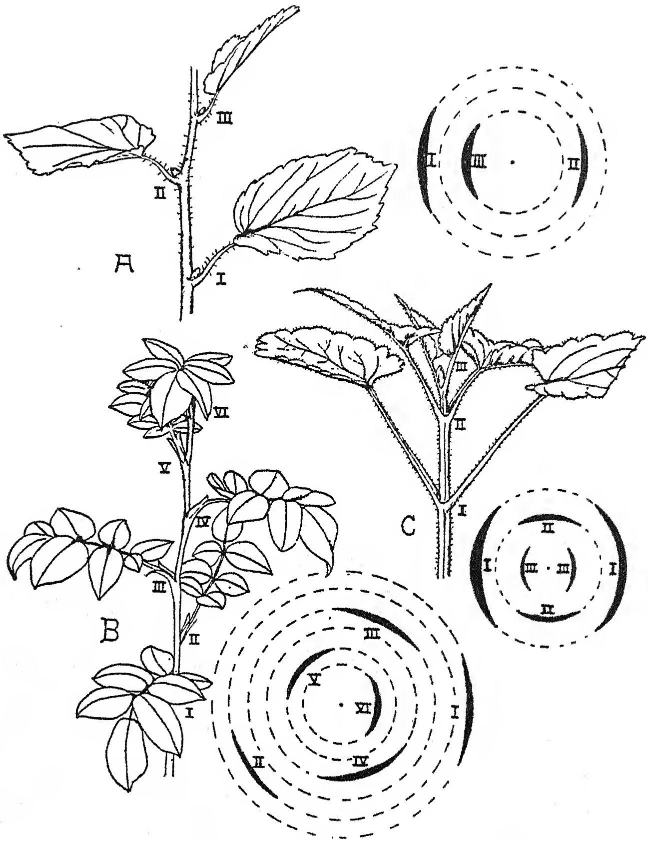

FIG. 70. Shoots and diagrams to show leaf-arrangement. A, Hazel (*Corylus*) (leaf-arrangement $\frac{1}{2}$). B, Dog-rose (leaf-arrangement $\frac{2}{5}$). C, Hedge Woundwort (*Stachys sylvatica*, leaf-arrangement decussate). In the diagrams the dotted circles represent successive nodes, the leaves being indicated in black and numbered in correspondence with the leaves on the shoots.

nodes is often not a constant one, so that, for instance, a $\frac{2}{5}$ arrangement below may give place to a $\frac{1}{3}$ above (*e.g.* in the Poplar). It is, however, important to realise that alternate leaves are not scattered irregularly on the shoot, but are disposed according to some definite, even though slightly variable, plan.

The external form of the stem often varies with the arrangement of the leaves upon it; thus, although in most plants having alternate leaves the stem is cylindrical, the $\frac{1}{3}$ arrangement in Sedges is associated with a triangular stem,

whilst in plants with decussate leaves the stem is often square (*e.g.* Labiatæ, Fig. 70, C; Scarlet Pimpernel).

The leaves of erect shoots or of rosettes retain throughout life the position which they occupied at their first development and which is generally well suited to prevent overshadowing. But on horizontal branches of trees and shrubs the conditions are different; the leaves show the same original arrangement as on the upright

FIG. 71. Photographs of two branches of the Hornbeam (*Carpinus*); on the left a horizontal branch showing leaf-mosaic, on the right an upright shoot showing radial arrangement of the leaves. [Photo. E. J. S.]

branches, but during development the position of the blades is altered and replaced by an arrangement more suited to the direction of illumination. This is very clearly seen, if one compares an upright and horizontal branch of a Privet or *Forsythia*. On the erect branch the decussate character is quite distinct, but on the horizontal one the leaf-stalks have twisted, so that the blades are placed more or less horizontally at right angles to the light, the original position of the leaves being only made out by a careful scrutiny of their mode of attachment.

The same feature can be observed in the Beech and Hornbeam (Fig. 71), where on the side-branches the leaves all appear in one plane instead of being radially disposed in a number of vertical

series. Whilst leaves are able to adjust their position in this way before they attain to maturity, this is not usually possible after the leaf is fully grown (see, however, p. 266); a position is therefore taken up during development, such as is well suited to light-reception.

The preceding considerations indicate that we must distinguish

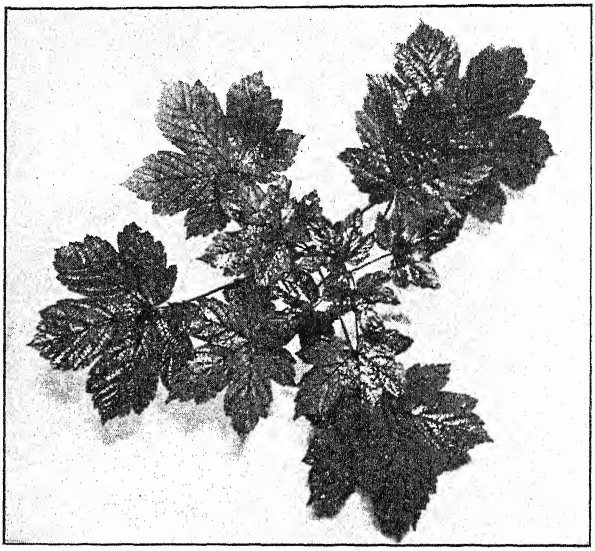

FIG. 72. Photograph of seedling Sycamore (*Acer pseudoplatanus*) taken from above, to show leaf-mosaic. [Photo. E. J. S.]

between the *radial* shoots of most erect plants in which the leaves and branches spread out in all directions from the axis, and *dorsiventral* shoots in which the leaves and branches lie in one plane, as in horizontal and creeping stems. In the latter, the axillary buds tend to grow out in the plane of the leaves, as in horizontal branch-systems of Hornbeam (Fig. 71), Elm, or Beech. Here there is an almost continuous expanse of leaf-surface, smaller leaves being situated between larger ones and those of neighbouring branches overlapping only to a very slight extent, so that we can speak of a *leaf-mosaic*. This feature is pronounced in trees with a dense canopy and in smaller plants growing in the shade of larger ones. Such leaf-mosaics are also exhibited by radial shoots (Fig. 72) and radical rosettes.

CHAPTER XII

LEAVES AND BUDS

THE foliage-leaf as a general rule consists of three parts: the base or slightly enlarged attachment to the stem, the stalk or petiole whose upper surface is generally grooved (Fig. 101), and the blade or lamina. Occasionally the petiole is absent (*sessile*,[1] *e.g.* Shepherd's-purse, Fig. 3, E), but the majority of leaves are *petiolate*. The petiole plays an important part, not only as an organ for spreading out the blade to the light and air, but also, as seen at the end of the last chapter, by placing the latter in the most suitable light-position.

The leaf-blade may consist of one continuous undivided surface, when it is described as *simple* (Fig. 73, A, B, E); or it may be cut up into a number of lobes connected with one another by an undivided portion, when the leaf is said to be *lobed* (Fig. 72; Fig. 73, D); or again it may be completely segmented into a number of separate leaflets, *i.e.* compound (Fig. 70, B; Fig. 73, C and H).

Diverse terms are used to describe the various shapes of leaves and leaflets. A prolonged description is, however, unnecessary, since Fig. 73 shows clearly what is meant by *linear* (*e.g.* Grass-leaves, Fig. 73, G), *lanceolate* (*e.g.* Privet, Fig. 73, I), *ovate* (*e.g.* Chickweed, Fig. 73, B), *obovate* (*e.g.* Garden Spurge, Fig. 73, F), *cordate* (*e.g.* Hedge Woundwort, Fig. 73, A), *reniform* (*e.g.* Ground Ivy, Fig. 73, E) and *hastate* (*e.g.* Convolvulus, Fig. 73, J). The obovate form is merely the ovate inverted, and similarly there are certain plants in which the blades have the shape of an inverted heart (*obcordate*, *e.g.* the leaflets of the Wood-sorrel, Fig. 173, p. 268). A peculiar type of leaf, termed *peltate*, is seen in the Pennyworts and the Garden Nasturtium (Fig. 117, B), the petiole being here attached to the centre of the round blade. A somewhat similar form occurs in the Garden Geranium (*Pelargonium*) in which the base of the lamina forms two lobes which almost meet in the middle line (*orbicular*). As a general rule the two halves of the blade are similar in size, but when one is larger than the other (*e.g.* Lime or Elm) the leaf is said to be *asymmetrical*.

Terms are similarly employed to describe the margin of the leaf; this may be either *entire* (Fig. 73, B, F, I), *i.e.* with a smooth uncut outline, or *serrate* (Fig. 73, A) with forwardly directed or *dentate* (*e.g.* Enchanter's Nightshade,

[1] Regarding the terms used in the description of plant-structure, see B. D. Jackson, *A Glossary of Botanical Terms.* Duckworth, 4th edit., 1928 (481 pp.).

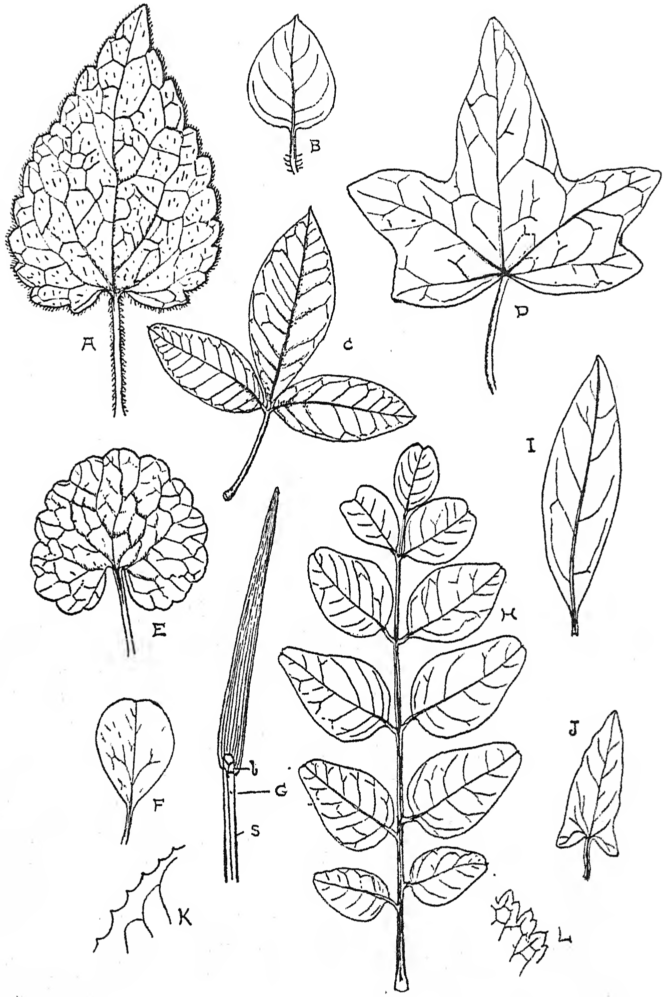

FIG. 73. Different types of foliage-leaves (all about one-half natural size). A, Hedge Woundwort (cordate, acute). B, Chickweed (ovate, acuminate). C, Laburnum (trifoliate). D, Ivy (palmately lobed). E, Ground Ivy (reniform, crenate). F, Garden Spurge (obovate, obtuse). G, Grass (linear). *l*, ligule; *s*, leaf-sheath. H, False Acacia (*Robinia*) (pinnate with mucronate leaflets). I, Privet (lanceolate, entire). J, Field Convolvulus (hastate). K, Enchanter's Nightshade (showing dentate margin only). L, White Dead-nettle (showing biserrate margin only).

Fig. 73, K) with outstanding teeth, or *crenate* (Fig. 73, E) with rounded projections. When the margin is provided with fine hairs, as in the Woundwort (Fig. 73, A) it is said to be *ciliate*, whilst when there are teeth of two sizes it is described as *biserrate* (*e.g.* White Dead-nettle, Fig. 73, L) or *bidentate*.

The nature of the leaf-tip also varies, but the figures will make quite clear what is meant by *acute* (Fig. 73, A and I), *obtuse* (Fig. 73, F), *acuminate* (*i.e.* tapering to a point, Fig. 73, B) and *mucronate* (*i.e.* with a small point arising from an almost straight edge, as in the leaflets of the False Acacia, Fig. 73, H). The surface of the leaf is either *leathery* (Laurel), without hairs (i.e. *glabrous*, Privet), *hairy* (Woundwort), or *glaucous* (*i.e.* with a waxy bloom, Sea Holly).

It was noticed in the Shepherd's-purse (p. 4, Fig. 3) that the extent of lobing of the leaf-blade varies greatly, and this shows that there is no essential difference between a serrate or crenate margin on the one hand and a deeply lobed margin on the other. In many plants, however, the character of the margin is quite constant, and therefore it is often convenient to employ special terms for deeply cut leaf-blades, *e.g.* the *sinuate* margin of the Oak or the *palmately lobed* leaves of the Ivy (Fig. 73, D) and Sycamore (Fig. 72), in which the lobes are arranged like the fingers of a hand.

There are two principal types of compound leaf: that in which the leaflets or *pinnæ* are arranged in two rows, one on either side of the leaf-stalk (*pinnate*, Fig. 73, H; Fig. 70, B), and that in which all the leaflets come off from the same point (*palmate*, as in the Lupine). In the former type the petiole either terminates in a leaflet (*e.g.* Ash, Rose, Fig. 70, B), or rarely such a terminal pinna is wanting. A common form of leaf is that shown by the Strawberry (Fig. 139) and Laburnum (Fig. 73, C), etc., in which only three leaflets occur, when the blade is said to be *trifoliate*. Occasionally the leaflets of compound leaves themselves exhibit subdivision, so that blades may be *bipinnate* (*e.g.* Beaked Parsley, *Acacia*, Fig. 174) or even *tripinnate* (*e.g.* many Ferns). Compound leaves are readily distinguished from branches bearing small leaves by the presence of a bud in the axil of the main stalk, by the absence of axillary buds to the individual leaflets, and by the absence of a terminal bud.

The transition of foliage already noticed in the Mallow (p. 37) indicates that the leaves of an individual are not necessarily all alike in form, and some plants indeed, as for instance the Ivy and the Scabious, regularly produce foliage of two types. In the former the lower leaves are palmately lobed, whilst those upon the flowering branches are more or less oval in outline.

As regards the arrangement of the veins (*i.e.* the *venation*) each leaf may show a prominent main vein or midrib, giving off a number of lateral veins which by continued branching form a network throughout the lamina (Fig. 3). Such *reticulate* venation is characteristic of the leaves of most Dicotyledons, but differences are found as regards the way in which the prominent veins are distributed. Most commonly a single midrib is predominant and

from it laterals of smaller size arise on each side (*pinnate* venation, Fig. 73, B and I and Fig. 365), but occasionally there are several veins of equal prominence branching out from the base of the blade like the fingers of a hand (*palmate* venation, Fig. 73, D and E). In most Monocotyledonous leaves a totally different type of venation is found; the blade is traversed by several veins of similar size running side by side and connected with one another by numerous cross-branches (*parallel* venation, Fig. 73, G).

The *leaf-base* [1] exhibits great variety of form and fulfils a number of different functions. In a large number of plants it appears merely as a more or less marked enlargement at the base of the leaf (*e.g.* Lime). This enlargement is sometimes extensive, forming a prominent cushion or *pulvinus*, and in such leaves the base often retains the power of bending throughout life, so that they are able to adjust their position repeatedly with reference to the light; examples are furnished by the pulvinus at the base of the petiole in the Runner Bean (Fig. 74, F, *p*) and at the base of the leaflets in the Wood-sorrel (Fig. 173). In these plants the leaflets change their position at night (cf. p. 268).

Plants possessing large blades often exhibit special modifications of the leaf-base which strengthen them to withstand sudden strain entailed by the resistance offered to wind and rain by the leaf-surface. A simple example is afforded by the Sycamore, in which this is met by a mere swelling of the leaf-base, but in a large number of plants (*e.g.* Burnet Saxifrage, Fig. 74, C, and other Umbelliferæ) the base is expanded to such a degree that it extends round the stem on either side as a more or less close-fitting *leaf-sheath* (Fig. 74, C, *l.b.*); in Grasses the margins [2] (Fig. 73, G, *s*) actually overlap. Since the lower edge of such a sheath is attached to the node along its whole circumference, a much firmer connection between leaf and stem is obtained without loss of elasticity. An extreme type is seen in the Sedges (*Carex*) where the leaf-sheath forms a closed tube enveloping part of the internode above, the blade, as in Grasses, actually diverging from the stem only at some distance above the node. A further increase of the connection with the stem is found in the Mullein (*Verbascum*, Fig. 74, G) and Cotton-thistle (*Onopordon*), where the lower part of the sessile blade is continued down the axis (*decurrent*).

In all plants in which the leaf-base is enlarged it affords a

[1] For details, see the work of Goebel, cited on p. 1.

[2] A peculiar structure, of varying size and shape and generally of a membranous texture, is present at the junction of blade and sheath in Grasses (Fig. 73, G, *l*). The purpose of this *ligule* is not properly understood, but it may be protective in function.

certain amount of protection to the axillary bud, and this is very pronounced in the swollen sheaths of Umbelliferæ (Fig. 74, C). A very efficient protection of axillary buds is shown by the Ivy (Fig. 61), the Plane-tree and the Syringa (Fig. 75, B), in all of which the hollow leaf-base more or less surrounds the bud, so that the latter is not visible until the leaf has been removed (see right-hand

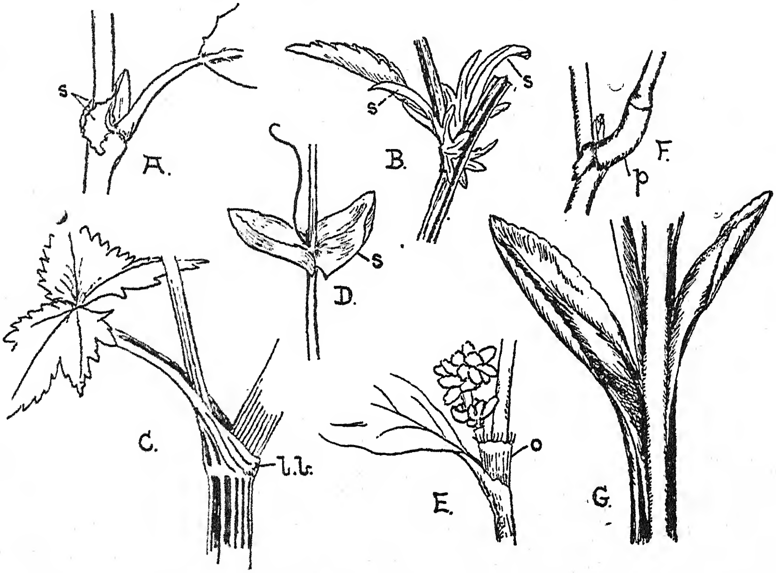

FIG. 74. Leaf-bases and stipules of various plants (all about natural size). A, Willow, summer-shoot. B, Pansy. C, Burnet Saxifrage (*Pimpinella magna*). D, Meadow Vetchling (*Lathyrus aphaca*). E, *Polygonum persicaria*. F, Runner Bean. G, Mullein (decurrent leaves). *l.b.*, leaf-base; *o*, ochrea; *p*, pulvinus; *s*, stipule.

diagram in Fig. 75, B). The value of the leaf-base as a protective structure depends in part on the fact that this portion of the leaf reaches maturity very early, and this is specially important in those plants in which it bears leafy outgrowths or *stipules* (Fig. 74, A and B) helping to shield the axillary bud. Leaves possessing such structures are described as *stipulate* in contrast to leaves in which they are absent, which are said to be *exstipulate*.

Simple forms of such stipules are found on the summer-shoots of Willows (Fig. 74, A, *s*) and in the Cherry, whilst larger ones, which are deeply lobed, are seen in the Pansy (Fig. 74, B, *s*). The Rose-leaf (Fig. 8, B, *s*; Fig. 70, B) has its stipules joined with the petiole, so that the base of the latter appears winged. In many plants the stipules are green and thus assist in the photo-

synthetic function of the blade; such stipules generally remain attached throughout the life of the leaf (*persistent*), whilst when merely protective they are often leathery or membranous and usually fall off at an early stage (*caducous*). Plants in which the blade is modified for other purposes (*e.g.* to form tendrils for climbing, as in the Meadow Vetchling, Fig. 74, D), often exhibit a

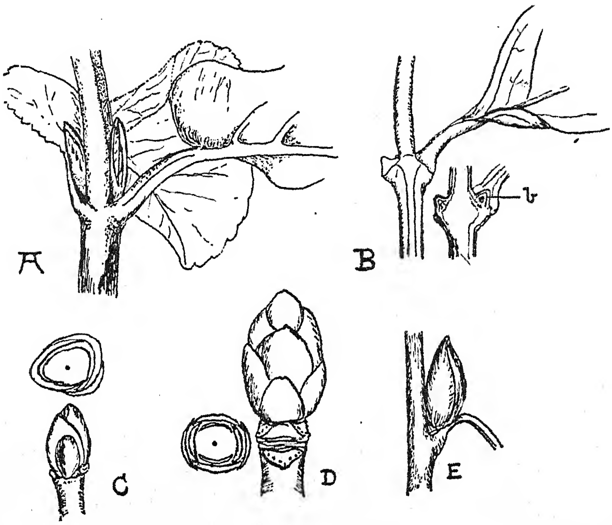

FIG. 75. Bud-protection (all figures about natural size). A, Wayfaring Tree (*Viburnum lantana*) (naked buds). B, Syringa (*Philadelphus*) (bud in hollowed petiole). C, Lime-bud, with plan of bud-scale arrangement above. D, Horse Chestnut-bud, with plan of bud-scale arrangement at side. E, Goat-willow (*Salix caprea*). *b*, bud.

great development of the stipules which then constitute the only photosynthetic portion of the leaf.

As a general rule stipules can be easily recognised as arising directly from the leaf-base, but occasionally they appear rather as outgrowths from the stem on either side of the node; they can, however, be distinguished from leaves by the fact that there is no bud in their axil. A very peculiar instance of this kind is furnished by the Goose-grass (Fig. 8, A) and the Bedstraws (*Galium*) in which each node appears to bear a whorl of leaves; but only two of these leaves situated opposite to one another ever possess axillary buds, and we can consequently infer that the other members of the whorl are stipules. The Persicaria (Fig. 74, E) and the Docks furnish other instances in which the stipules are not at once obvious, since here they are joined together so as to form a short membranous

tube (*ochrea*) surrounding the axillary bud and the base of the internode above.

Material for the study of the early development of the shoot is furnished by every bud. The essential structure is always the same and may for the sake of convenience be examined in a Brussels Sprout,[1] a bud in which, owing to its large size, all the parts are easily recognised. Outwardly we see merely a series of overlapping leaves, but a more complicated structure is presented when the bud is halved lengthwise (Fig. 76). The central portion is occupied by the axis which tapers to the meristem (*g.pt.*) above. Below the latter are seen series of developing leaves (p', p'', p''', etc.), the youngest and smallest nearest the meristem, the oldest and most advanced farthest from it. A very short distance behind the meristem minute buds (*ax.b.*) are seen arising in the axils of the young leaves and, farther from the apex, the buds become more and more prominent until each is recognised as having the structure of the whole in miniature. The young leaves are closely crowded together and the upper internodes are scarcely developed; consequently there is insufficient room for the enlarging leaf-blades which become thrown into numerous folds, and thus the familiar compact structure of a bud is developed.

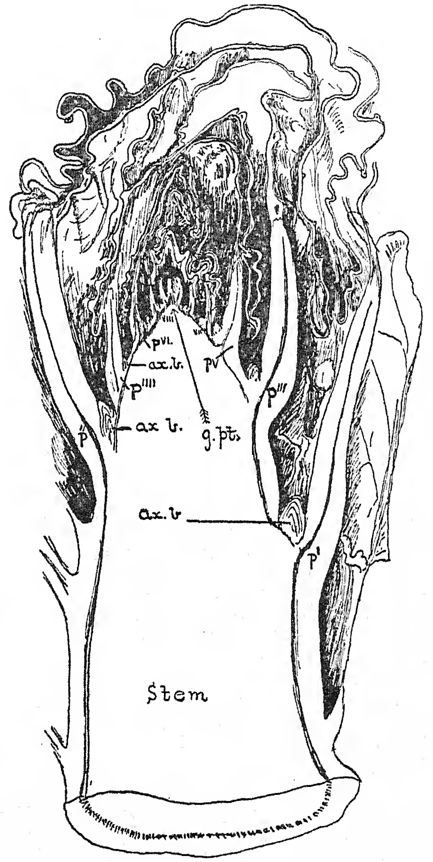

FIG. 76. Section of Brussels Sprout (*Brassica oleracea*) (considerably enlarged). *ax.b.*, axillary buds; *g.pt.*, meristem of main axis; p', p'', p''', etc., leaves of successive ages.

[1] The Cabbage is likewise a huge bud, each Brussels Sprout being a Cabbage on a small scale.

The Brussels Sprout is an example of a summer-bud in which the close packing gives sufficient protection to the young structures developing within, although even here the whole is enveloped in maturer leaves. In buds which have to withstand the rigour of winter additional protection is, however, necessary and this is provided in a number of different ways. Most commonly the bud is covered in by close-fitting leathery or membranous scales (the *bud-scales*), which are frequently brown (*e.g.* Beech, Oak), but sometimes black (*e.g.* Ash), and usually exhibit the same arrangement as the leaves upon the stem (Fig. 75, C and D).

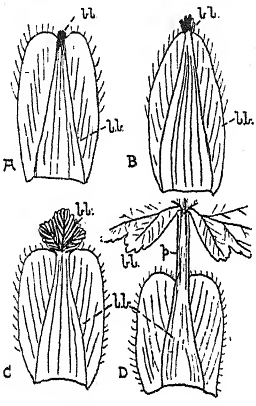

FIG. 77. Transition between bud-scales and foliage-leaves in Flowering Currant (*Ribes sanguineum*); the successive stages are marked A–D and are all about twice natural size. *bl.*, blade; *l.b.*, leaf-base; *p*, petiole.

At first sight a bud-scale appears to differ very much from a foliage-leaf, but a comparative examination of the parts of the opening buds of the Flowering Currant will enable us to deduce that the one is but a modification of the other. If, starting at the outside, the bud-scales are removed in succession, a gradual transition will be found between them and the foliage-leaves within the bud (Fig. 77). The outermost scales are oval with a minute black apex (Fig. 77, A, *bl.*); a little farther in, the scales show a somewhat larger tip which on careful scrutiny is seen to be a rudimentary or arrested leaf-blade (Fig. 77, B, *bl.*); still farther in, the latter becomes more prominent (Fig. 77, C), and so by successive stages we come to the first foliage-leaves in which a petiole (Fig. 77, D, *p*) appears and in which the scaly enlargement at the base (*l.b.*) shows a diminution in size. In the innermost leaves of the bud this scale is seen to have contracted into a small leaf-base, such as is found in the mature foliage-leaves of the plant. All these transitions may not be present in a single bud.

The bud-scales of the Flowering Currant are therefore nothing else than modified leaves with a much enlarged leaf-base and a more or less completely arrested lamina. The same deduction can be made regarding the bud-scales of the Sycamore, Ash, Horse Chestnut, etc. It is not always the whole leaf-base, however, that forms the bud-scale, for a study of opening buds of the Beech (Fig. 78) or Elm will show that caducous stipules are the protecting structures. Whereas the inner scales are seen to arise in pairs

from the bases of the unfolding leaves, a variable number of the outer scales, though likewise paired, have no corresponding blades. As in the buds of the Flowering Currant, therefore, the laminæ of the outermost leaves are arrested, only the part necessary for protection (here the stipules, there the leaf-base) being represented.

Another type of bud-scale is seen in the Lilac and Privet in

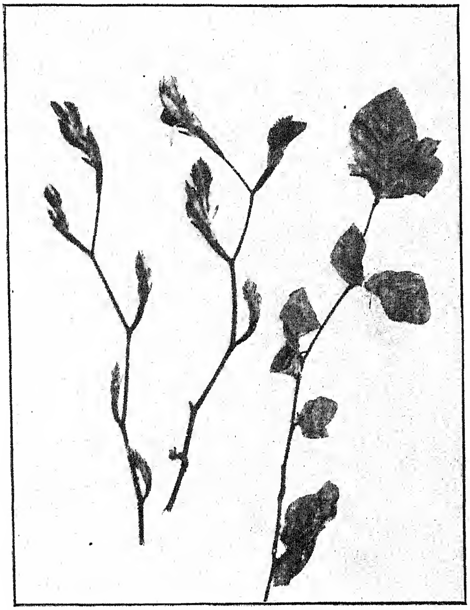

FIG. 78. Photographs of Beech-twigs showing successive stages of bud-expansion. In the right-hand twig the stipular bud-scales can be seen adhering to some of the foliage-leaves. [Photo. E. J. S.]

which, if the structures composing the bud are removed in succession, it will be found impossible to say exactly where to draw the line between bud-scale and foliage-leaf. In fact the bud-scales here are entire leaves of small size and leathery consistency. In the Willow the two bud-scales (Fig. 75, E) represent the first leaves of the shoot (p. 37). The bracts found in the region of the inflorescence (p. 427) are frequently modified structures comparable to bud-scales, often representing an enlarged leaf-base with a rudimentary lamina at the apex (e.g. *Helleborus*).

Bud-scales are not always the only special protection of the winter-bud, for not uncommonly there is a layer of sticky varnish (*e.g.* Horse Chestnut, Poplar), which further reduces the risk of excessive transpiration (cf. pp. 8 and 13) from the young leaves

within. Moreover, the latter are often equipped with numerous protective hairs, appearing as a white wool in the Horse Chestnut or as a dense brown covering in the Plane Tree (p. 159). A few plants, of which the Wayfaring Tree (Fig. 75, A) and the Alder Buckthorn (*Rhamnus frangula*) are the only British examples, rely solely on such a felt of hairs, their buds being naked without enveloping scales.

Returning to the study of the Brussels Sprout we may follow up the stages in the development of the foliage-leaf. Even with a lens, some of the leaf-rudiments nearest the meristem appear as perfectly uniform structures, as yet showing no signs of the three parts of the mature leaf. Farther from the apex a distinction can be made between leaf-base and leaf-blade. It is only at a much later stage of development that intercalary growth takes place between the two regions resulting in the formation of the short petiole.

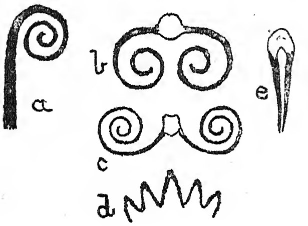

FIG. 79. Diagram to explain method of folding of the young foliage-leaves; in all cases the blade is shown in section. *a*, Fern. *b*, Violet. *c*, *Polygonum*. *d*, Lady's Mantle (*Alchemilla*). *e*, Laurel. In *b–e* the lower surface of the leaf is shown uppermost.

If we examine the buds of a number of different plants, we shall find that the way in which the young foliage-leaves are folded varies greatly (see Fig. 79, B–E). These folds often persist to some extent, for a brief period, after the leaf has emerged from the bud (*e.g.* Beech, Lady's Mantle, etc.), the young blade thus not exposing its full surface until the tissues have matured.

With the arrival of spring all the different parts within the bud begin to expand, the hitherto short internodes commence to lengthen and the leaves to unfold, this taking place at the expense of the food-materials which are stored up in the woody branches (p. 13). As a result the whole bud swells (Fig. 78), the bud-scales are forced apart, and the shoot begins to elongate. No lengthening of the internodes between the bud-scales usually takes place; they consequently remain as a crowded group at the base of the growing shoot. Sooner or later they drop off, leaving a number of broad flat scars which, on superficial observation, look like a series of closely set rings encircling the stem; since such *bud-scale scars* (see Fig. 67) are necessarily formed only at the beginning of each season, the intervals between successive series mark as many years' growth of the branch.

The shoot is generally in an advanced state of development

within the bud, in some early flowering plants (*e.g.* Lilac, Horse Chestnut, Flowering Currant) even including an inflorescence in which most of the parts are already present in miniature; the changes subsequent to opening are chiefly in the direction of a rapid increase in size of the different organs. In trees and shrubs most of this growth takes place in a few weeks, and during the remainder of the summer the buds (terminal and lateral) for the next year are being constructed. The enlargement of the shoot-system in a given season is therefore more or less dependent on the nature of the preceding one, and this applies especially to the extent of flowering in those plants in which the flowers are already formed in the winter-buds; of the latter many fruit-trees afford excellent examples.

CHAPTER XIII

THE STRUCTURE OF THE YOUNG STEM

STEMS, as contrasted with roots, develop under very diverse conditions as regards mechanical strains, illumination, supply of moisture, etc., and correlated with this display a much more varied structure. The general plan of construction of the stem differs from that of the root in several important respects.

The organisation of a Dicotyledonous stem[1] can be studied in a cross-section through the uppermost internode of a young Sunflower (Fig. 80, A). The most obvious feature is that the vascular tissue is a ring broken up into distinct *vascular bundles*. In each the thick-walled xylem (*xy.*) is towards the inside and the thin-walled phloem (*ph.*) towards the outside, the two thus lying on the same radius (constituting a *collateral* bundle), in contrast to the alternate arrangement of these tissues obtaining in the root. By the disposition of the vascular bundles in a ring the ground tissue is marked out into three regions, namely, the *cortex* (Fig. 80, A, *c.*), the *rays* (*r.*), and the *pith* (*p.*). The terms *pith*, *cortex*, and *rays* are, however, purely topographical, and do not necessarily imply any differentiation between the component cells, which in fact are largely thin-walled and parenchymatous in all three regions (cf. Fig. 82, *Co.* and *p.*). The edge of the section is bounded by the *epidermis*[2] which differs from that of the root in having strongly thickened outer walls. It forms a continuous layer except where interrupted by the presence of stomata or lenticels (p. 189). Its function is to protect the more delicate internal tissues, and in correspondence with this it does not wither at an early stage like the piliferous layer. Occasional cells grow out into hairs (Fig. 80, *A*, *h.*), but these are quite different in character from the root-hairs.

Immediately within the epidermis in this stem are several layers of collenchymatous cells (Fig. 80, A, *s.*), thickened mainly on the tangential walls, whilst between the cells of the inner layers are

[1] Reference-books on plant-anatomy are listed on p. 100.

[2] For a detailed consideration of epidermis and stomata, see the [illegible] chapter.

relatively large intercellular spaces. Such spaces are also abundant in the ground tissue generally, and appear as small triangular cavities between the polygonal cells of the pith.

At the inner limit of the cortex there is a single layer of cells distinguished by the frequent presence of large starch-grains (Fig. 82, *sh.*), which can be rendered more prominent by staining with iodine. The layer in question bends outwards around each vascular bundle, and so presents a sinuous outline. Such a *starch-*

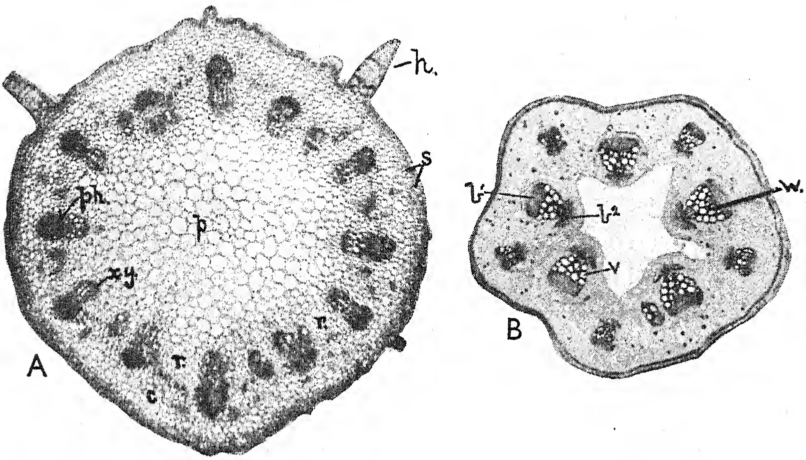

FIG. 80. Photomicrographs of transverse sections of A, the young stem of the Sunflower (*Helianthus*); B, of the Marrow (*Cucurbita*). b^1, b^2, phloem; *c.*, cortex; *h*, hair; *p.*, pith; *ph.*, phloem; *r*, rays; *s*, collenchyma; *v*, vessel; *w*, wood; *xy.*, xylem.

sheath is not uncommon in herbaceous Dicotyledonous stems (cf. also Fig. 103, *S.s.*). The central cylinder, which is separated off from the cortex by this sheath, is termed the *stele*, and comprises the vascular bundles and the accompanying ground tissue.

The zone of tissue between the starch-sheath and the phloem constitutes the *pericycle*, which, in the Sunflower, is composed of groups of fibres (not fully thickened in the young internode) opposite the bundles (Fig. 81, *f.*; Fig. 103, *F*), and elsewhere of parenchyma (Fig. 80, A). In other plants the pericycle is often parenchymatous throughout, consisting of one or more layers of cells. The term, as in the root, is a purely topographical one, being applied to the region situated between the conducting strands and the starch-sheath or a similar continuous layer of cells.

In the individual bundles the phloem can be distinguished by the shining appearance of the cell-walls, which resemble those of

the young fibres, as well as by the unequal size of its component elements (Fig. 81). The large, empty-looking sieve-tubes, exhibiting an occasional sieve-plate (*s.p.*) [1] and associated with small companion cells (*c.c.*), which have dense contents, are intermingled with ordinary parenchyma-cells (*phloem-parenchyma*, *ph.p.*). Two or three layers of flattened thin-walled cells, situated between the phloem and the xylem, constitute the region of the *cambium*

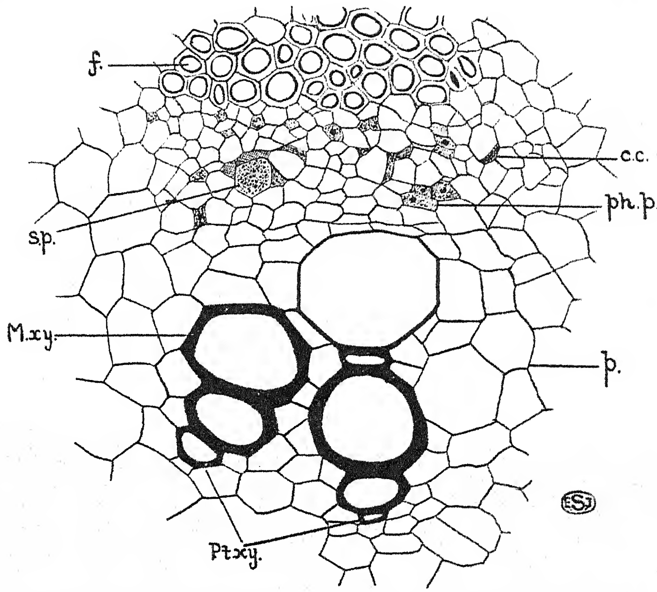

FIG. 81. A single vascular bundle from the stem of the Sunflower (*Helianthus*) in transverse section. *c.c.*, companion cells (shaded); *f.*, fibres of the pericycle; *M.xy.*, metaxylem; *p.*, parenchyma of the rays; *ph.p.*, phloem-parenchyma; *Pt.xy.*, protoxylem; *s.p.*, sieve-plate.

(cf. Fig. 103, *C*, p. 171), a meristematic zone which becomes active in the older stem and forms additional vascular tissue (cf. Chapter XVI).

The wood consists of radial files of vessels separated by rows of smaller parenchymatous cells (the *wood-parenchyma*, Fig. 81). The vessels (*Pt.xy.*), situated nearest the pith, are the *protoxylem* (cf. p. 67), while the larger metaxylem-elements (*M.xy.*) are towards the outside, a further point of contrast to the root. The wood-parenchyma cells have more or less thickened walls, which are lignified like those of the vessels, but they nevertheless retain their living contents. Small cells resembling the wood-parenchyma,

[1] The sieve-plates are not readily recognised in the Sunflower.

but not lignified, form a sheath (the *medullary sheath*, Fig. 80, A) at the inner edge of each bundle.

A longitudinal section of a Sunflower-stem passing radially (*i.e.* parallel to a radius) through one of the bundles will show the same succession of tissues and enable us to complete our picture of the various elements (Fig. 82). The short and somewhat bulging epidermal cells are succeeded by those of the collenchyma, which are many times longer than broad, and have strongly

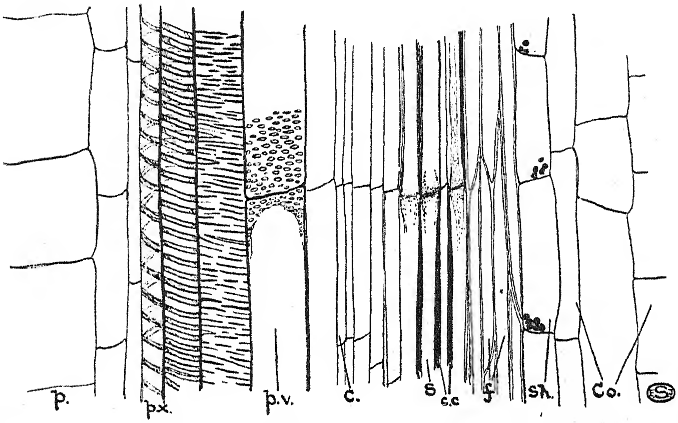

FIG. 82. Longitudinal section through a vascular bundle of the Sunflower (*Helianthus*). *c.*, cambium; *c.c.*, companion cells; *Co.*, cortex; *f.*, fibres of pericycle; *p.*, pith-parenchyma; *p.v.*, pitted vessel of metaxylem; *px.*, spiral vessel of protoxylem; *s.*, sieve-tube; *sh.*, starch-sheath.

thickened longitudinal walls (cf. Fig. 39, A, of Dead-nettle). The thin-walled rectangular cells of the cortex (Fig. 82, *Co.*) are much shorter. Next come the starch-sheath (*sh.*), recognisable by its large starch-grains, and the typical fibres of the pericycle (*f.*). The detailed structure of phloem and cambium (*c.*) will be studied in another stem, but in the former the long, apparently empty, sieve-tubes (*s.*) and the narrow, densely granular, companion cells (*c.c.*) are readily distinguished. The vessels of the metaxylem (*p.v.*) bear very dense spirals or occasionally bordered pits, whilst in the protoxylem the thickening takes the form of rings or of a loose spiral (*px.*). The narrow elongated elements sometimes seen between are the wood-parenchyma cells.

Further insight into the structure of the Dicotyledonous stem will be afforded by a study of that of the Vegetable Marrow (*Cucurbita*) (Fig. 80, B; 83). The transverse section differs from that of the Sunflower in the hollow pith, in the presence of a broad ring of

sclerenchyma (*Scl.*) some little way beneath the epidermis, and in the arrangement and construction of the vascular bundles. A pith-cavity is a frequent feature in the stems of herbs (*e.g.* Labiatæ, Umbelliferæ, Gramineæ, etc.), and can be related to cessation in the growth of the pith-cells, so that rupture occurs as a result of the continued enlargement of the stem.

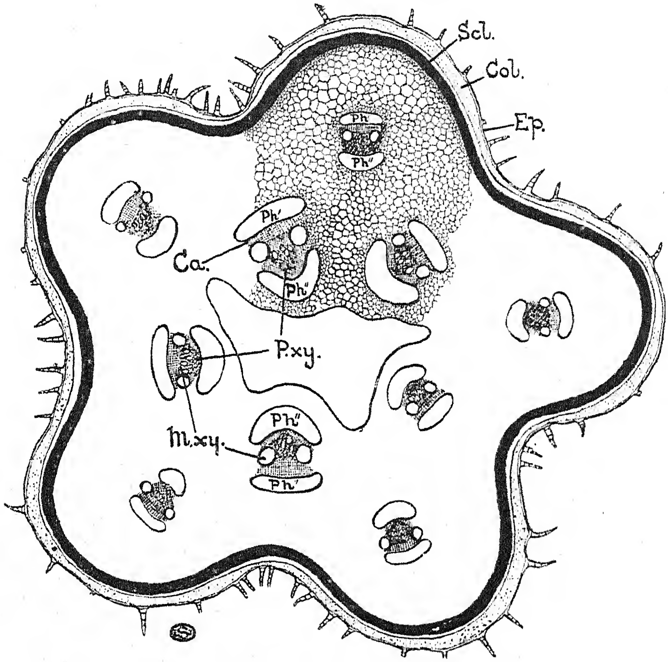

FIG. 83. Diagram of a transverse section of the stem of the Vegetable Marrow (*Cucurbita*). *Ca.*, cambium; *Col.*, collenchyma; *Ep.*, epidermis; *M.xy.*, metaxylem; *Ph.'*, outer phloem; *Ph.''*, inner phloem; *P.xy.*, protoxylem; *Scl.*, sclerenchyma (black).

In the stem of the Marrow there are two rings of vascular bundles of which the larger and inner alternate with the smaller and outer (Fig. 83). Two groups of phloem occur in each bundle, one external (*Ph.'*), separated from the xylem by the cambium (*Ca.*), the other internal (*Ph.''*), separated from the protoxylem (*P.xy.*) by ordinary parenchyma or sometimes by a second cambium. Such bundles, termed *bicollateral*, are not uncommon in certain families of Flowering Plants, such as the Cucurbitaceæ (to which the Marrow belongs), and the Solanaceæ, and offer a marked contrast to the normal collateral type seen in the Sunflower. The elements of

both xylem and phloem are remarkably large, and are therefore especially suited for a study of their detailed structure, which can be rendered more distinct by staining with eosin (see Appendix IV).

In the *phloem* many of the large somewhat thick-walled sieve-tubes appear empty; but here and there, where the plane of section coincides with a separating wall, there is a deeply stained sieve-plate (Fig. 36, *s.p.*), recognisable by its dotted structure. Under the high power the sieve-plate exhibits an irregular network of thickening, completely covered by a thin layer of cytoplasm, the greater part of each mesh being occupied by an open pore through which communication with the next segment of the sieve-tube is established. In contact with each sieve-tube are one or more small, often more or less triangular companion cells (Fig. 36, *c.c.*), with dense contents. The numerous phloem-parenchyma cells (Fig. 36, *p.*) are more or less intermediate in size, but without either the thickened wall of the sieve-tube or the dense contents of the companion cell. Both inner and outer phloem show the same structure.

In longitudinal sections (Figs. 36, left, and 84) the horizontal sieve-plates (*s.p.*), stained red with the eosin, occur at frequent intervals in the course of the sieve-tubes. When viewed in optical section, they present an interrupted appearance, due to the alternation between the pores and the bars of thickening with their covering of cytoplasm. Functionless sieve-like areas are sometimes present as isolated patches on the longitudinal walls (cf. Fig. 36, left). Thick, highly refractive masses, composed of a carbohydrate known as *callose*, are often found on one or both sides of the sieve-plates. Such deposits of callose, bringing about a closure of the latter, arise sooner or later in the sieve-tubes of most plants, and are often permanent, marking the end of the activity of the element in question; in some woody plants and in many Monocotyledonous rhizomes this is, however, a periodic phenomenon, the callose being formed in the autumn and becoming redissolved at the advent of spring. Callose is distinguished by being insoluble in ammoniated copper oxide, but soluble in a 1 per cent. solution of caustic potash, and by its reddish-brown colouration with chlor-zinc-iodide; it becomes deeply stained by eosin or a dilute aqueous solution of aniline blue, which should be allowed to act for half an hour.

Here and there the plane of the section passes through a companion cell (Fig. 36, *c.c.*) in contact with its sieve-tube. The former tapers off towards the sieve-plates above and below, so that its length coincides with that of the sieve-tube segment from which it was cut off. The large nucleus can generally be seen embedded in the dense cytoplasm which completely fills the cell. The phloem-parenchyma cells (Fig. 36, *p.*) are readily distinguished by their

shape from the other elements. The cells of the cambium (Fig. 84, *Ca.*) appear much elongated in the longitudinal section and have chisel-shaped ends.

In the transverse section of the *wood* one can recognise, as in the Sunflower, small protoxylem-elements towards the interior (Fig. 83, *P.xy.*), large metaxylem-vessels beyond (*M.xy.*), and numerous intermingled wood-parenchyma cells. Where two vessels are in contact, the middle lamella between the pitted thickening layers of

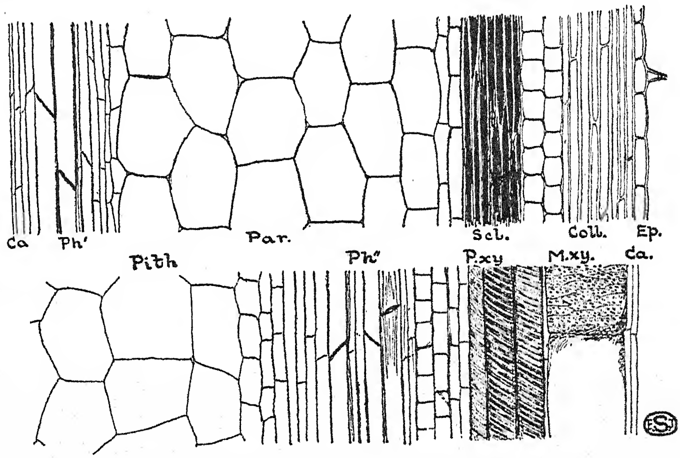

FIG. 84. Longitudinal section through the stem of the Vegetable Marrow (*Cucurbita*). *Ca.*, cambium; *Coll.*, collenchyma; *Ep.*, epidermis; *M.xy.*, metaxylem; *Par.*, parenchymatous cortex; *Ph.'* and *Ph."*, outer and inner phloem; *P.xy.*, protoxylem; *Scl.*, sclerenchyma. The right-hand end of the lower figure joins on to the left-hand end of the upper.

the common wall can be clearly made out. In longitudinal sections the broad metaxylem-vessels (Fig. 84, *M.xy.*) show reticulate thickenings which are in marked contrast to the spiral thickenings of the protoxylem-vessels (*P.xy.*); the slight constrictions occurring at short intervals mark the limits of the vessel-segments, and, in thick sections, the ring-like remnants of the original septa can often be distinguished. The exceptionally large vessels are a marked feature of many other climbers besides the Vegetable Marrow.

Stems of Monocotyledons (of which the Maize furnishes a typical instance) usually exhibit a large number of bundles which frequently appear scattered throughout the whole of the ground tissue, so that a definite cortex and pith cannot be distinguished, *i.e.* there is often no sharply circumscribed stele as in the ordinary Dicotyledon. The bundles (Fig. 85, A), though differing in certain details, show the same general structure, being collateral

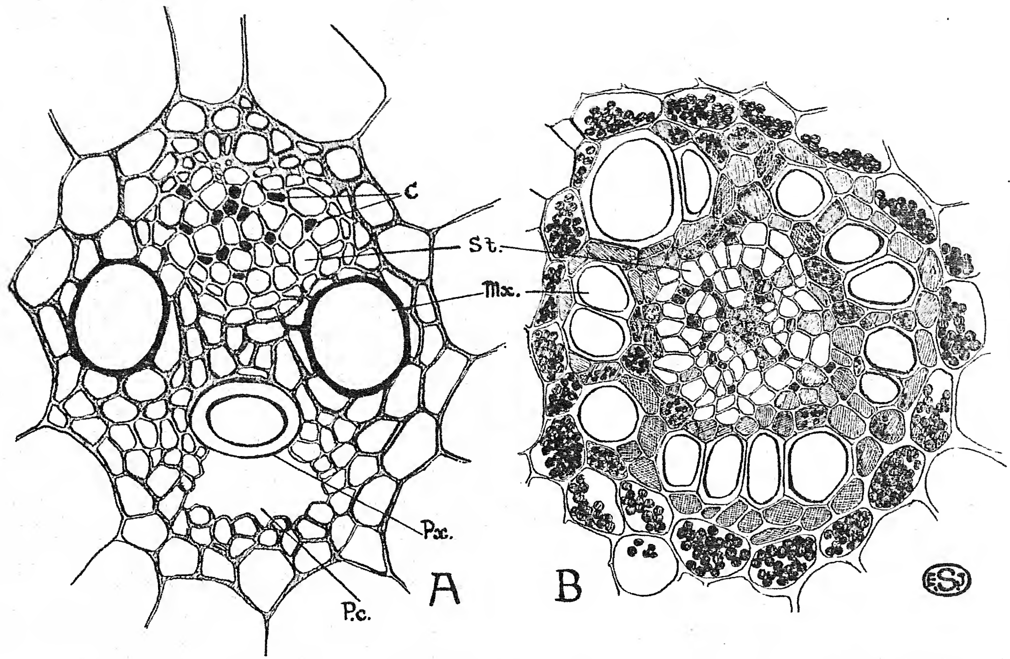

FIG. 85. Vascular bundles of the Maize (*Zea mais*) (A) and the Sweet Flag (*Acorus calamus*) (B). *C.*, companion cells; *Mx.*, metaxylem; *P.c.*, protoxylem canal; *Px.*, protoxylem; *S.t.*, sieve-tubes. Note the envelope of thick-walled cells surrounding the bundle of the Maize.

with xylem and phloem on the same radius and with the protoxylems (*p.x.*) directed inwards.

The phloem (Fig. 85, A), which often has similar shining cell-walls to that of the Sunflower, is an oval or rounded group of tissue composed of sieve-tubes (Fig. 85, A, *S.t.*) and small companion cells (*C.*). The latter are more rounded than is usual in Dicotyledons, and this, combined with the absence of parenchyma,[1] leads to the remarkably uniform appearance of the phloem. There is no cambium between the xylem and the phloem, an important respect in which the Monocotyledonous bundle usually differs from that of the Dicotyledon. The shape of the xylem as a whole is often roughly that of a Y, the stem of which is occupied by a radial row of protoxylem-vessels (Fig. 85, A, *Px.*), whilst the arms are formed by a pair of large metaxylem-vessels (*Mx.*). The phloem tends to be sunk between the latter (cf. Fig. 85, A), but the degree of sinking varies considerably in different stems, and in extreme instances the phloem may even be completely surrounded by the xylem (as in the Sweet Flag, *Acorus calamus*, Fig. 85, B). As usual, a certain amount of wood-parenchyma occurs between the vessels. In the stems of the Maize and many other Monocotyledons which exhibit rapid elongation, the protoxylem-vessels undergo early rupture and give rise to an irregular cavity (cf. p. 68) (Fig. 85, A, *P.c.*), in which remnants of the spiral or annular thickenings are recognisable. The bundles are commonly enveloped in a sheath of small, thick-walled cells (often fibres, *e.g.* in the Maize, Fig. 85, A), a feature also encountered in some Dicotyledons (*e.g.* Buttercup).

The typical Monocotyledonous stem thus differs from that characteristic of Dicotyledons in the large number, scattered arrangement, and general form of the bundles, in the usual absence of a cambium, and in the detailed structure of the phloem.

Certain Dicotyledons (*e.g.* Buttercup and its allies), however, show resemblance to Monocotyledons in the shape of the bundle, in the absence of phloem-parenchyma, and the very feeble development of the cambium. Moreover, the stem of the Dicotyledon may exceptionally possess a relatively large number of scattered bundles (*e.g.* Meadow Rue, *Thalictrum*), whilst that of Monocotyledons may in its turn exhibit a ring-like arrangement of the bundles (*e.g.* Black Bryony, *Tamus*, Fig. 86) and a feeble development of cambium (cf. p. 170).

In certain Dicotyledons which possess a normal ring of vascular bundles additional ones occur in the pith (*e.g.* Spinach, *Oenanthe crocata*) or cortex (e.g. *Buxus sempervirens*). Such *medullary* and *cortical* bundles are often probably merely strands entering from the leaves which have not yet taken their normal place in the vascular cylinder (cf. p. 168). These bundles either show

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[1] Phloem-parenchyma is present in some Monocotyledons.

the normal orientation (*i.e.* with the xylem towards the inside), or they exhibit the reverse arrangement; in many plants, moreover, they consist of phloem only.

The way in which the stem fulfils its functions may now be considered. The elements of the xylem and other mechanical tissues such as collenchyma, whilst giving some support to the young stem, are by themselves inadequate to confer rigidity in the young condition. This is readily seen when plants in a vase droop for want of water. Since, however, they again become

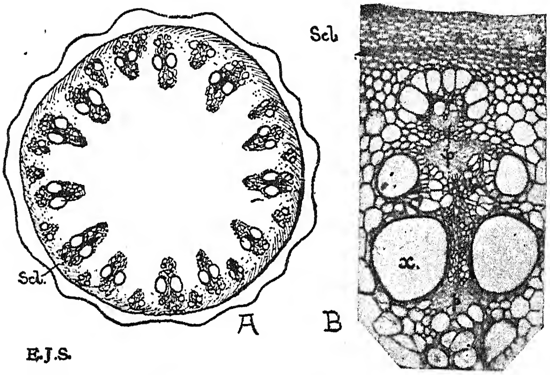

FIG. 86. Stem of the Black Bryony (*Tamus communis*). A, Diagram of transverse section. B, Photograph of a small portion on a larger scale. *p.*, phloem; *Scl.*, sclerenchyma-ring; *x.*, metaxylem vessel.

erect when a fresh supply is added, an observation which can be made in nature on any hot summer's day, the obvious conclusion is that a proper supply of water is necessary for rigidity. As we have seen, every living cell of a healthy plant is turgid, so that it is as firm as an inflated cycle-tyre or a toy balloon. The plant being largely composed of such turgid cells, the whole forms a stiff structure which only becomes flaccid when water is deficient. Part of the liquid can be readily withdrawn from the turgid cells by placing herbaceous plants (*e.g.* any seedling) in a strong solution of salt for some minutes, when they become quite limp, though subsequent immersion in water restores the original firmness.[1]

[1] The recovery of a flaccid shoot when water is sucked into it can be demonstrated with the help of the apparatus shown in Fig. 122 (p. 200), by using a one-holed rubber cork on the flask, provided with a piece of glass tubing bent as in the figure. The upper end of the flaccid shoot is removed and the cut surface, thus produced, is attached to the long arm of the glass tube, whilst the lower end of the shoot is placed in water. In order to prevent the entry of air by way of the stomata, both surfaces of the flaccid leaves should be vaselined. As a consequence, the suction generated within the flask (cf. p. 199) operates in causing a rapid flow of water through the shoot. After a short time the leaves become turgid.

There is a further aspect of turgidity that plays an important part in the stability of the herbaceous plant. To study this point we select young shoots of the Elder (or in winter the flowering stems of Narcissus or Daffodil) and cut off a piece about 8 inches long with straight ends. The hard outer portion is then completely removed in four longitudinal strips leaving only the juicy central pith of the stem. If we now compare the length of the original piece with that of one of the outside strips and with that of the pith, we shall find that the former is a little shorter and the latter slightly longer. This indicates that in such a stem the pith is in a state of compression, whilst the outer tissues are in a state of tension. The advantage of this condition, known as *tissue-tension*, can be shown in the following way.

A weak spiral spring (such as can be made by twisting thin steel wire round a piece of wood), about 8 or 9 inches long, and a similar length of an inner tube of a cycle-tyre are obtained. Neither is capable of supporting itself when erect; if, however, the spring is slipped into the rubber tube and the former slightly compressed, so that the ends of the tube can be firmly tied, the two combined form a structure of considerable rigidity. Here, just as in the stem, the inner part is in a state of compression while the outer is extended.

It is in consequence of such tissue-tensions that many herbaceous shoots, when halved lengthwise, exhibit a curvature of the two halves with the exterior on the concave and the interior on the convex side; similarly the cut ends of the flower-bearing stalks of Dandelions and other plants, when kept in water, split from below upwards into two or more portions, each coiling up with the inner side facing outwards.

The shoot of the erect plant is chiefly liable to bending, and thus contrasts with the root, which is exposed chiefly to pulling strains. When a stem is bent, the tissue on the convex side is stretched out, whilst that on the concave side is pressed closer together, and the farther we pass from the centre the greater will be the extension and compression respectively. Hard tissue situated at the outside therefore renders a stem best able to withstand bending; and since the strains to which a shoot is subjected, as a result of the force of wind and rain against the leaves, may operate in any direction, the advantage of an equal and symmetrical distribution of the strengthening tissue on all sides is obvious. Related to this the *mechancial tissues* of the stem are more or less symmetrically arranged near the periphery. In the young stem the upright position is maintained by the combined support afforded by sub-epidermal collenchyma (Figs. 38, 80, and 83),

the xylem, and the turgidity of the living cells. As the stem matures, additional mechanical tissue is often furnished by the development of pericyclic fibres (*e.g.* Sunflower, Fig. 81, *f.*), of a thick-walled sheath to the bundles (Monocotyledons, Fig. 85, A; Buttercup), or of a zone of sclerenchyma in the cortex (*e.g.* Vegetable Marrow, Fig. 83, *Scl.*). Even in the ordinary Monocotyledonous stem the bundles are far more numerous near the edge; moreover, Monocotyledons frequently exhibit a copious development of peripheral sclerenchyma, to which, for instance, the hardness of a

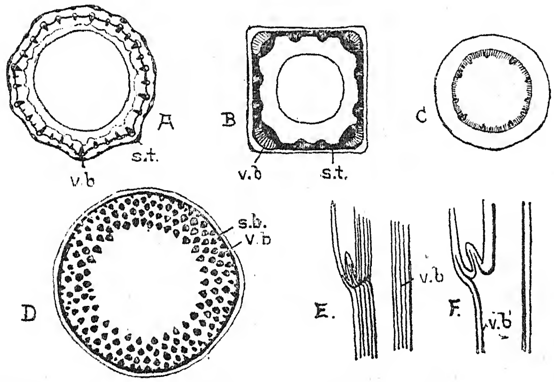

FIG. 87. Diagrams of stem-structure. A–D, cross-sections (considerably enlarged). A, Bishop's-weed (*Aegopodium*). B, *Stachys*. C, Dicotyledon stem with continuous ring of wood. D, *Asparagus*. E–F, longitudinal sections through stem, leaf, and axillary bud; E of *Asparagus*, F of *Stachys*. *s.t.*, non-vascular supporting tissue; *v.b.*, vascular strands.

Bamboo is largely due. The presence of mechanical elements immediately beneath the epidermis often results in a ribbed or fluted appearance of the stem (as in many Umbelliferæ, Fig. 87, A), whilst in the Labiatæ (Fig. 87, B) this strengthening tissue forms a continuous square tube in which the vascular strands themselves are embedded.

In slender underground stems aiding in the attachment of the plant, and therefore chiefly exposed to tension, a much more centralised disposition of the mechanical elements is observed than in the upright shoot. This is well seen in many Sedges and Grasses. An extreme condition is reached in water-plants, where, owing to the prevalent pulling strain, such mechanical tissue as is present becomes concentrated at the centre of the stem (cf. p. 543).

Most young stems exhibit *chloroplasts* in the cortical cells (even when these are collenchymatous, as in the Campion), the carbon dioxide requisite for photosynthesis being obtained from the intercellular spaces between them, which communicate with the atmo-

sphere by means of occasional stomata in the epidermis. The outer cortical zone sometimes (*e.g.* Umbelliferæ) consists of alternating bands of mechanical and photosynthetic tissues, the former occupying the ridges, the latter situated beneath the furrows. Here the stomata are restricted to the strips of epidermis overlying the photosynthetic tissue.

Varied evidence (p. 199) shows that the vessels are the channels by which water and mineral salts are passed from the root into the leaves. The phloem, on the other hand, probably conducts elaborated food-substances, the proteins appearing to travel mainly by way of the sieve-tubes. If, for instance, the stem of the Vegetable Marrow be dipped into boiling water so as to coagulate the contents, the abundant proteins in the sieve-tubes can be demonstrated by heating longitudinal sections with Millon's reagent. The storage of food-substances in perennial organs (*e.g.* rhizomes, tubers, etc.) is effected chiefly by the thin-walled ground tissue.

Whilst it has been seen that the arrangement of the tissues differs materially in root and stem, the ground tissues in the two organs pass over imperceptibly into one another. The protoxylem-strands are directly continuous, whilst the metaxylem is developed towards the exterior in the stem and towards the interior in the root, and occupies a more or less intermediate position in the region (*i.e.* the hypocotyl) where the *transition* from the one to the other type of structure takes place. The phloem is similarly continuous, and the transition from root to stem mainly involves a lateral and outward displacement accompanying the enlargement of the vascular cylinder (Fig. 88). The transition between the two organs is, however, often very complex, being accompanied by splitting or union of conducting strands, as a result of which the number of protoxylem-groups in stem and root do not necessarily correspond.

The development of the different regions of the axis from the meristems has already been described in Chapter VI, but some additional details as to the manner of origin of the vascular tissues will serve to amplify the picture. These first appear in the axis a short distance behind the tip as so-called *procambial strands*, composed of very narrow, elongated, thin-walled cells with tapering ends, dense protoplasmic contents, and prominent nuclei. They develop by repeated longitudinal division of certain cells of the meristem, in which transverse division almost ceases at an early stage, the narrow segments thus formed subsequently elongating.

In the stem each procambial strand gives rise to a vascular bundle, whilst in the root there is usually a single strand from which the whole vascular cylinder is differentiated. The innermost

elements, in each of the procambial strands of the stem, become the spirally thickened protoxylem-vessels, whilst simultaneously the outermost elements develop into the first-formed phloem (*protophloem*). As the strands are traced farther and farther from the apex (*i.e.* from younger to older stages) the differentiation of xylem and phloem proceeds towards the middle of each. Ultimately all that remains is a narrow strip of thin-walled cells between xylem and phloem, which in Dicotyledons gives rise to the cambium.

In many Dicotyledons (*e.g.* woody types), however, the procambium forms a continuous cylinder which is produced either as a result of enlargement and confluence of the procambial strands or by the intercalation of accessory strands. As a consequence primary xylem and phloem, interrupted by narrow rays, may already in the young stem form concentric cylinders. Not uncommonly pericyclic fibres originate from the outer part of the same procambial strand as produces vascular tissues. In the root alternating groups of protoxylem and protophloem arise at the periphery of the procambial strand, whilst the later-formed elements and the pith, if present, develop from the central region.

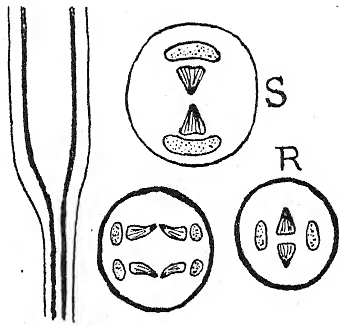

FIG. 88. Diagrams showing one type of transition from the vascular structure of the root to that of the stem. The dotted areas represent phloem and the shaded xylem; protoxylem shown black. *R.*, root; *S.*, stem; the remaining cross-section, hypocotyl.

Both leaves and branches originate close behind the apex of the stem as superficial outgrowths (*i.e.* are *exogenous*, Figs. 30, 31), a mode of development contrasting markedly with the internal (endogenous) origin of lateral roots. The protection afforded to the latter as a result of their internal origin is unnecessary for the branches of the stem. Leaf-rudiments, at first, consist merely of a mass of periblem enveloped by a protrusion of the epidermis (Fig. 31), but as they enlarge procambial strands are formed within them by division of certain cells. The differentiation of these strands gradually extends inwards till they ultimately join those of the stem. As a result the vascular bundles of leaf and stem are continuous in the mature condition (p. 168, Fig. 102). When vascular strands occur in the stipules they are branches of those in the leaf-base. The strands arising in the young branches also become connected with those in the stem.

CHAPTER XIV

THE EPIDERMIS

THE surface of the shoot is protected by the epidermis, composed of one layer of living cells which possess certain marked characteristics. In transverse sections the cells usually appear somewhat flattened with slightly convex outer walls; moreover, they fit closely together without intercellular spaces (Figs. 42 and 89, *Ep.*). The epidermal cells have living contents, usually contain plastids, and possess large vacuoles filled with watery, generally colourless, sap (Fig. 89, *Ep.*). Chloroplasts are not developed in the cells in well-illuminated situations, but are often present in the epidermis of submerged aquatics or of land-plants when growing in the shade (cf. pp. 522, 550).

The outer epidermal walls are usually more strongly thickened than the others, and so changed (*cuticularised*) as to render them much less permeable to water vapour and gases. The exact nature of the modification is obscure, but it appears to consist essentially in impregnation with substances of a fatty character; these are most abundant in the outermost region of the external walls, which together form a relatively impermeable layer, continuous over the whole epidermis (except for the stomata), known as the *cuticle* (Figs. 89 and 92, *Cu.*). Where the walls are strongly thickened an intervening zone (the cuticularised layers), in which cuticularisation has not progressed to the same extent, can sometimes be distinguished between the cuticle and the unaltered cellulose on the inside. The cuticle is often yellowish in colour, whilst the cuticularised layers, when present, appear faintly yellow and less transparent than the colourless cellulose. The cuticle may be quite smooth, but in some leaves (e.g. *Helleborus fœtidus*) it presents numerous minute ridges which appear as faint striations in surface sections. Cuticularisation may sometimes extend to the lateral walls, which then are generally thickened, so that in section they appear as pegs projecting inwards.

The cuticle is insoluble in cuprammonia and concentrated sulphuric acid, being the only part of the epidermis that does not

dissolve in the latter reagent. With iodine and sulphuric acid it yields a brown colouration, and it is easily stained with Scharlach red, probably as a result of the presence of fatty substances.

Owing to its toughness, the cuticle, especially when strongly developed, renders the epidermis more efficient as a protection against mechanical injury and infection; but its chief function is

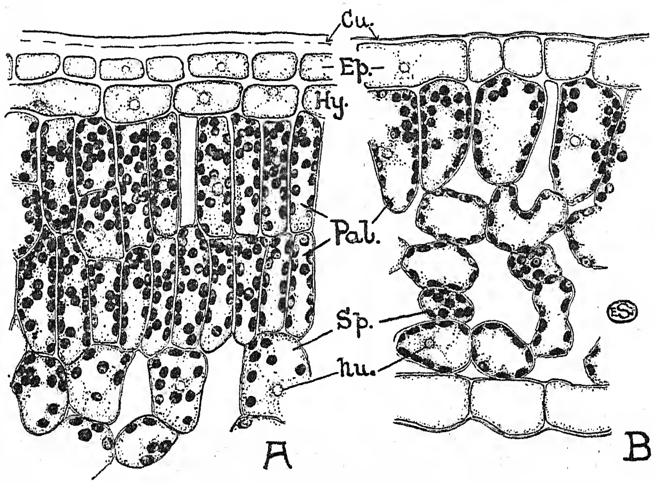

FIG. 89. Transverse sections through the leaves of the Holly (A) and *Ranunculus auricomus* (B). In the former only half of the vertical extent of the leaf is shown. *Cu.*, cuticle; *Ep.*, epidermis; *Hy.*, hypodermis; *Nu.*, nucleus; *Pal.*, palisade layers; *Sp.*, spongy parenchyma. The chloroplasts are shown black.

to restrict transpiration mainly to the stomata. In correspondence with this its thickness varies with the nature of the habitat; thus the cuticle is most strongly developed in plants of dry situations (*e.g.* Gorse, Fig. 345, B; *Psamma*, Fig. 397, A, etc.), whilst it is extremely thin in or absent from submerged aquatics (Fig. 382), where absorption of water takes place over the whole surface. Most young organs, before they have attained their full size, possess but a very thin cuticle and exhibit considerable cuticular transpiration; hence the necessity for other means of reducing water-loss (*e.g.* hairs, folding of leaves, etc.). Even a very thick cuticle is, however, not completely impermeable. Its efficiency in reducing transpiration is sometimes augmented by a covering of *wax* secreted by the epidermal cells; when present in any considerable quantity (*e.g.* leaves of the Sea Holly, fruit of the Plum, etc.), this gives the surface a bluish tinge. Such coverings of wax also

prevent the collection of moisture on the surface of the plant. They are readily rubbed off, but may be subsequently renewed.

Not uncommonly the epidermis can be easily stripped off and so examined in *surface view*, when it will again be seen to form a continuous layer (Fig. 90, B–D) without intercellular spaces, the only gaps being the pores of the stomata. The shape of the cells in such surface sections is very varied. In stems (Fig. 90, D) and in the leaves of most Monocotyledons (Fig. 90, C) they are usually considerably elongated parallel to the longitudinal axis, whilst in most Dicotyledonous leaves they are roughly isodiametric (Fig. 90, B). Where the lamina is thin the lateral walls of the epidermal cells are often undulated (Fig. 90, B). Through this wavy outline the cells interlock, so that the surface of contact is increased, and the risk of tearing by the wind is diminished. The lower epidermis, which has numerous points of weakness constituted by the stomatal perforations, generally exhibits this undulation to a more marked degree than the upper.

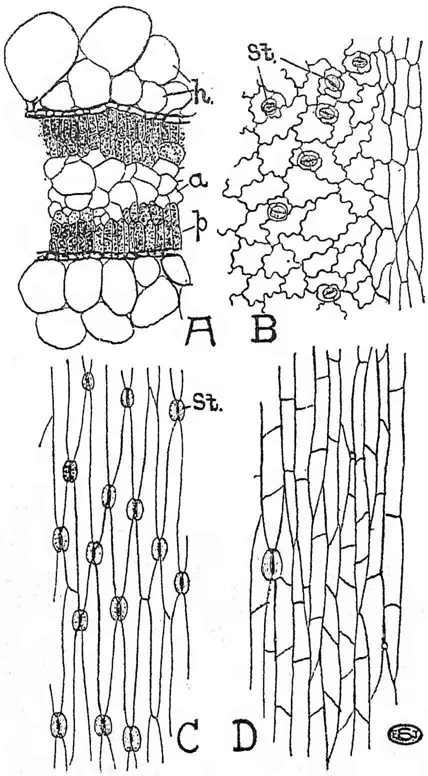

FIG. 90. Structure of the epidermis. A, Transverse section of leaf of Silver Goosefoot (*Obione portulacoides*) showing the bladder-like hairs (*h.*), the aqueous tissue (*a.*), and the palisade layer (*p.*). B, Surface section of leaf of Ground Ivy (*Nepeta glechoma*). C, Surface section of leaf of Onion. D, Surface section of stem of Runner Bean (*Phaseolus multiflorus*). *St.*, stomata.

The epidermis in the young plant keeps pace with the increasing size of the underlying tissues by the division and growth of its cells, but usually all the septa are at right angles to the surface, so that it remains a single layer. This subdivision is plainly recognisable

in the stem of the Runner Bean, where the spindle-shaped epidermal cells, after reaching a certain size, become divided by transverse septa (Fig. 90, D).

In plants of dry habitats the epidermal cells may attain a considerable size (*e.g.* in the Sea Purslane, *Arenaria peploides*) and serve for the storage of water, which is possibly always a function of this layer, though here to a much greater extent than normally. In extreme instances water may be stored in localised enlargements, which often project as water-containing *hairs* or bladders (*e.g.* the Ice-plant, *Mesembryanthemum crystallinum*, and the Silver Goose-foot, *Obione portulacoides*, Fig. 90, A, *h.*). In times of drought the adjacent photosynthetic tissues withdraw moisture from these cells, which consequently contract, the side walls becoming undulated; when water again becomes plentiful, the cells fill and the walls gradually straighten out. The epidermis is not uncommonly aided in the storage of water by the development of one or more additional layers, which may be formed by the division of the dermatogen (*Ficus elastica*), or by differentiation from the underlying periblem (as in the Holly, Fig. 89, A, *Hy.*). The cells of such a *hypoderm* resemble the epidermal cells in the possession of large vacuoles and the absence of chloroplasts, but usually have thinner walls. It will hence be realised that leaf and young stem are always surrounded by a water-jacket tending to diminish the heating effect of the sun.

Water may also be retained by thick mucilaginous internal walls (cf. p. 70) developed by the epidermal cells (*e.g.* Hollyhock, Sycamore, etc.). These often project deeply into the photosynthetic tissues when swollen with water. This feature tends to retard the evaporation of water during periods of drought.

The pronounced thickening and cuticularisation of the outer walls of the epidermal cells, and the absence of intercellular spaces between them, endues the epidermis as a whole with considerable strength. It hence serves as a mechanical protection, but also (in combination with the hypoderm, when present) as a light-screen for the underlying chlorophyll. Moreover, the polished cuticle, especially characteristic of tropical plants, serves to reflect a large part of the light and heat rays falling upon it. Most important of all, it checks evaporation from the general surface of the plant, and indeed, where the cuticle is thick, transpiration is almost entirely restricted to the stomata.

Certain *modifications* of the epidermis are associated with special physiological functions. Thus in many shade-loving plants the outer walls of the epidermal cells are markedly convex (*e.g.* Wood Sorrel; Moschatel, *Adoxa*, Fig. 91). Each cell, then,

functions as a plano-convex lens focussing a localised patch of bright light at its base. It has been suggested that this acts as a mechanism for the orientation of the leaf, since, when the direction of illumination is altered, the position of the patch of light likewise changes. The protoplasm upon which this light falls is assumed to be sensitive, so that an adjustment of the leaf follows until the patch of light is again located in the normal position. But quite apart from any value that this may possibly have in enabling the plant to place its leaves at an appropriate angle to the light, the concentration of the latter may well be of value in connection with photosynthesis.

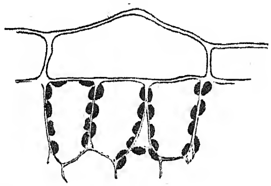

FIG. 91. Transverse section through part of the upper epidermis and palisade layer of the leaf of the Moschatel (*Adoxa moschatellina*). The chloroplasts are shown black.

The general characteristics of *stomata* are readily studied by stripping off a piece of the epidermis from a fresh leaf of the *Iris*. Scattered among the colourless elongated cells are oval stomata, each consisting of two bean-shaped *guard-cells* (Fig. 92, C, *g.c.*; see also Fig. 90, C) surrounding the narrow elliptical *pore* by means of which the intercellular spaces of the leaf communicate with the external atmosphere. The guard-cells contrast with the ordinary epidermal cells in containing numerous chloroplasts and starch-grains, and are especially distinguished by the uneven thickening of their walls, which are thin on the side away from the pore, but markedly thickened around the latter. Each guard-cell has a well-developed protoplast and a prominent nucleus. The ordinary epidermal cells almost meet above the guard-cells, so that the latter are only plainly visible on focussing to a lower level (Fig. 92, C); in this way the pore comes to be situated at the bottom of a miniature hollow (*vestibule*) constituted by the surrounding cells, and the stoma consequently occupies a sheltered position. This feature is especially marked in plants of dry situations, but in those growing in damp, shady habitats the guard-cells are often level with or raised above the adjacent epidermis (Fig. 345, C, D).

The overarching of the guard-cells by the adjoining epidermal cells is equally obvious in a transverse section (Fig. 92, D) of the *Iris*-leaf. Here each guard-cell appears approximately oval in form and provided with thick walls, the thickening being especially marked adjacent to the pore, and giving rise to a slight upwardly projecting ridge at the outer edge of the aperture. In many plants, however, the walls of the guard-cells are not so uniformly thickened,

those remote from the pore being relatively thin, whilst those towards the aperture show a marked decrease in thickness opposite the middle of the pore (*e.g.* Onion, Fig. 92, E); in such stomata the outer ridges are well marked, and there is frequently a second pair of ridges on the inner side. As a result of this unequal distribution of the thickening, the cavities of the guard-cells taper abruptly in the direction of the pore, so that a maximum thickness is obtained

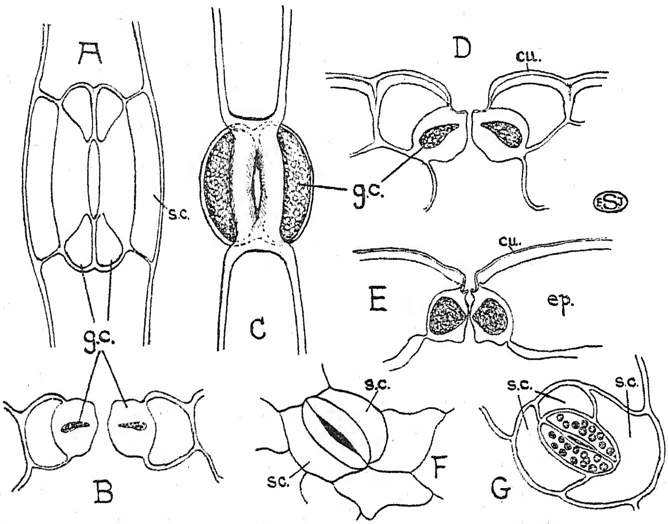

FIG. 92. Structure of stomata. A, C, F and G, in surface view; B, D and E, in transverse section. A, B, Millet-Grass (*Milium effusum*). C, D, *Iris germanica.* E, Onion (*Allium cepa*). F, Madder (*Rubia peregrina*). G, *Sedum spectabile.* *cu.*, cuticle; *ep.*, epidermal cell; *g.c.*, guard-cells; *s.c.*, subsidiary cells.

towards the upper and lower sides (Fig. 92, E); in some plants this is so marked that the whole cavity merely appears as a slit (*e.g.* Grass, Fig. 92, B). Beneath the stoma lies an air-space, the *respiratory cavity* (Fig. 98, *R.*), serving for the immediate interchange of gases and water-vapour between the intercellular system of the plant and the air around.

The vertical leaf of the *Iris*, in which both surfaces are alike, bears almost the same number of stomata on each. Moreover, the latter are all placed parallel to the axis, as in most Monocotyledons (Fig. 90, C) and the epidermis of young stems; in the latter, however, the stomata are often few in number (Fig. 90, D). Those of horizontal dorsiventral leaves (*e.g.* most Dicotyledons) are chiefly situated on the lower surface, being sometimes altogether

absent from the upper (*e.g.* most trees), and, moreover, exhibit an irregular arrangement (Fig. 90, B).

The number of stomata per unit area apparently bears no relation to the need for economy of water. Actually the frequency of stomata for a particular species may vary greatly in different parts of the same leaf, and especially in leaves growing under different conditions. The frequency appears to depend almost entirely on the species concerned and the extent to which the stomata are separated by the growth of the intervening epidermal cells, and as a consequence the leaves of plants growing in dry habitats usually have more numerous stomata than those of the same species when growing in humid conditions (cf. p. 522).

TABLE OF STOMATAL NUMBERS

	Average Upper Epid.	Average Lower Epid.
TREES		
Oak (*Quercus Robur*)	0	450
Beech (*Fagus sylvatica*)	0	236
Birch (*Betula alba*)	0	184
SHRUBS		
Barberry (*Berberis vulgaris*)	0	400
Hazel (*Corylus avellana*)	0	225
Whortleberry (*Vaccinium myrtillus*)	16	120
Elder (*Sambucus nigra*)	0	90
Guelder Rose (*Viburnum opulus*)	0	79
HERBS		
Brachypodium sylvaticum	240	0
Wild Hyacinth (*Scilla nutans*)	55	51
Daffodill (*Narcissus pseudo-narcissus*)	65	68
Dog's Mercury (*Mercurialis perennis*)	0	82
Lesser Celandine (*Ficaria verna*)	21	75
Goldielocks (*Ranunculus auricomus*)	16	59
Lilium martagon	0	30
AQUATICS		
Water Plantain (*Alisma plantago*)	50	36
Water Forget-me-not (*Myosotis palustris*)	7	91
Frog Bit (*Hydrocharis morsus-ranæ*), floating leaves	89	0

The stomatal apparatus originates from a mother-cell which is cut off by means of a curved septum from one of the ordinary epidermal cells. Soon a vertical wall is formed parallel to the long axis of the mother-cell, separating the future guard-cells, which gradually acquire their distinctive thickening. Meanwhile the middle lamella between them breaks down, except at the two ends, to form the pore. In some families the guard-cells are accompanied by so-called *subsidiary cells* (two in the Rubiaceæ,

Fig. 92, F, *s.c.*, three or more in the Crassulaceæ, Fig. 92, G, *s.c.*) which differ in size and shape from the other epidermal cells, and probably form part of the mechanism of the stoma. Subsidiary cells are usually cut off from the mother-cell before the guard-cells are produced, but in some plants they are formed by division of the surrounding epidermis.

On mounting a strip of fresh epidermis in water, the open pores of the stomata are conspicuous, being usually occupied by air. On transference to glycerine or a 5 per cent. sugar solution, which will reduce the turgor of the guard-cells, the width of the pores decreases appreciably (*i.e.* they "close"), but when returned to water the turgor is restored and they again open. Measurement shows that, though there is usually no marked change in length, there is an appreciable increase in width, when the stoma opens (cf. Fig. 93). The alteration in form of the guard-cells, to which the variation in the size of the stomatal aperture is due, is thus primarily determined by changes in turgescence.

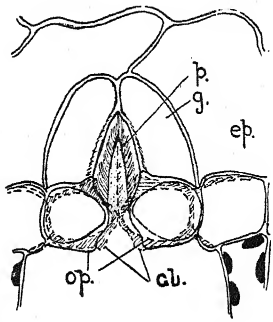

FIG. 93. Half of a stoma seen in perspective, showing the positions of the guard-cells in the open (*op.*, firm lines) and closed (*cl.*, dotted lines) conditions. *ep.*, epidermis; *g.*, guard-cell; *p.*, pore.

The *mechanism* is, however, directly dependent on the unequal distribution of thickening which, in transverse section, has been seen to be mainly localised around the upper and lower edges of the pore; on the other hand, the middle of the convex wall next to the pore, as well as the curved wall remote from the pore, remain comparatively thin (Fig. 92, E). When the guard-cells are turgid and the thin walls stretch, the pull exerted separates the thick walls, thus opening the pore (Fig. 93, *op.*). As seen in section, opening of the stoma is accompanied by a flattening of the convex walls on each side of the pore and an increased convexity of the unthickened walls. As a result there is movement of the guard-cells at the lines of junction with the adjacent epidermis both above and below, due to the bulging of the walls away from the pore. Where both the outer and the inner walls of the epidermal cells are thickened, there is at the points of junction with the guard-cells a sudden thinning which admits of their movement (*e.g.* Onion, Fig. 92, E); but when the external wall alone is thickened, such a hinge occurs only on the outside (*e.g.* Iris, Fig. 92, D). The flattening of the convex walls adjacent to the

pore is facilitated by the thinner middle portion, which constitutes a similar hinge.

An illustration of an action analogous to that of a stoma and depending likewise on unequal distribution of thickening can be obtained in the following way. A straight piece of Daffodil-scape or of the internode of a Dog's Mercury, about 3 to 4 inches long, is halved lengthwise, the two halves being then placed in a strong solution of salt until they become flaccid (p. 143). They are thereupon placed parallel to one another with the original outer surfaces in contact, while what was previously the inner surface is directed outwards. In this position the two halves are firmly tied together at their two ends. If the two pieces thus joined are placed in water, they will, as they again become turgid, arch apart so as to leave a wide aperture between them—in other words, the pore of our artificial stoma opens. A return to the salt-solution will once more result in a closure, and this sequence of events can be repeated.

The *influence of external conditions* on the size of the stomatal pore can be indirectly studied by means of an instrument known as the *porometer*. This may be constructed as follows (Fig. 94):—A short length of stiff thick-walled rubber tubing (about $\frac{1}{4}$ inch bore) is cut off square, and one end is melted by placing it against a heated metal plate. On cooling, the sticky end (*a*) is pressed against the under side of a leaf (*l*) still on the plant. The other end is connected with the arm of a glass T-tube (*t*). To the other horizontal arm is attached about two inches of thin rubber tubing (*d*), which is closed by a clip (*c*), and to the vertical arm of the T-tube a twelve-inch glass tube (*e*) is connected at *b*, with its open end in a beaker of water. By opening the clip and applying suction at *f* the water is raised in *e*. The clip is now closed and the water-column in *e* will be seen to fall. This is due to the passage of air from the stomates of the uncovered part of the leaf through the air-spaces into the tube *t*. According as the aperture of the stomates is wide or narrow the water-column falls rapidly or slowly. By attaching a scale to the back of *e*, the rate of fall of the water through a given distance can be estimated. While the rate of fall of the water varies with changes of stomatal aperture, it is clearly also dependent upon the resistance to flow of air through the intercellular spaces of the leaf which may likewise undergo change.

A more direct method is that adopted by Lloyd: Leaves, growing in the particular conditions to be studied, are detached from the plant and immediately placed in strong alcohol, which fixes the guard-cells in their momentary condition. A strip of epidermis can now be removed without alteration, and the average size of the stomatal apertures directly measured under the microscope (cf. Appendix II). Such measurements can also be made on the living plant.

Either of these methods will serve to demonstrate the tendency of the stomata (except in many shade and marsh plants, *e.g.* the Water Plantain, *Alisma plantago*) to "close" when the shoot becomes flaccid owing to deficiency of water, although they may open more widely at the first commencement of wilting. "Closure" commonly accompanies a change from light to darkness, which emphasises the fact that alteration in turgidity of the plant as a whole is not necessarily involved. It may be noted that Fungi, which have no stomata, also exhibit diminished transpiration in darkness. The sensitiveness of the stomatal mechanism is so

great that even the effect of temporary shading, as by a big cloud, can be observed with the help of the porometer. Moreover, shaking may cause a more or less marked temporary "closure," and it is best to allow a short interval to elapse, after fixing the porometer, before readings are taken.

The rate of transpiration depends alike upon the water-content and temperature of the leaf and upon external factors (*e.g.* wind, humidity, etc.). Though the stomata ultimately respond to wilting, their closure is often too delayed and they may be ineffective. Under normal conditions the falling water-content of the leaves reduces the transpiration-rate, but in strong winds, etc., this adjustment is quite inadequate. The amount of transpiration decreases with increased humidity, but does not become zero even in saturated air.

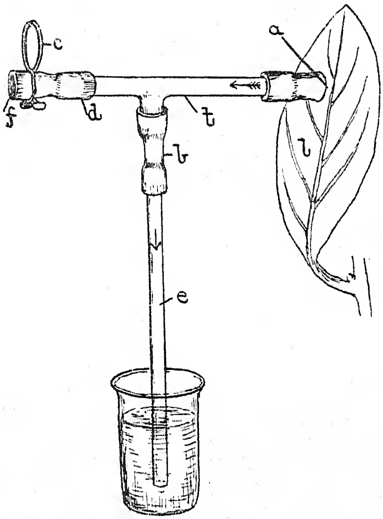

FIG. 94.—Porometer, for description see text.

The response of stomata to changes in illumination is largely due to alterations in the relative proportions of starch and sugar in the guard-cells controlled by a diastatic enzyme (p. 83). In light, starch is hydrolysed, the sugar-content and osmotic strength of the sap increase, and the stoma opens; in darkness, the process is reversed and the concentration falls. When open, the osmotic concentration of the guard-cells may be five times that when "closed." Other factors are, however, involved, such as the reaction of the cell-sap which affects the permeability of the cytoplasm and its capacity to imbibe water.

A much modified type of stoma is found in the Gramineæ and Cyperaceæ (Sedge-family), though the mechanism is essentially similar. The much elongated guard-cells surround a large pore having the form of a flattened hexagon (Fig. 92, A). In the middle portion of each guard-cell the outer and inner walls are so strongly thickened as to leave only a small slit-shaped cavity (Fig. 92, B), but the end-portions are thin-walled and somewhat enlarged (Fig. 92, A, *g.c.*). On either side of the stoma is a thin-walled subsidiary cell (*s.c.*). These latter, together with the terminal

portions of the guard-cells, function in much the same way as the thin-walled part of an ordinary guard-cell, whilst the thick median portions correspond to the thickened walls of the latter.

Not uncommonly a few, or even many, of the epidermal cells (cf. Fig. 83) grow out into more or less elongated, often branched, processes called *hairs*, which are especially common on leaves and,

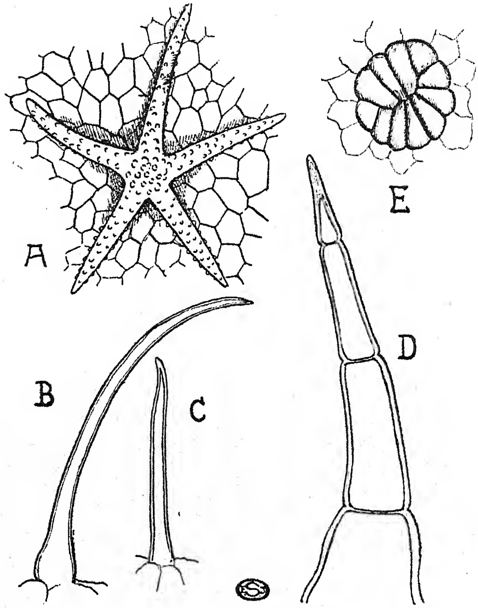

FIG. 95. Hairs. A, of *Deutzia*; B, of *Cynoglossum*; C, of Shepherd's Purse (*Capsella*) (unbranched type); D, of Vegetable Marrow (*Cucurbita*); E, of Hop (*Humulus*).

when numerous, very obvious. They may remain unicellular (Fig. 95, B, C), or become multicellular (Fig. 95, D) by the formation of septa. Nearly every type of hair, whether branched or not, may be, in one plant or the other, uni- or multi-cellular without any appreciable difference in outward form; but the presence or absence of septa, as well as the structure of the hair, are often characteristic of whole groups. The walls of the hairs are of varying thickness, and either consist of cellulose or have undergone chemical alteration.

One of the most important *functions* of hairs, when numerous, is to bring about a decrease in the rate of transpiration in wind. The moist air entangled between these hairs is sheltered, so that

it is not readily removed by air-currents, nor does it diffuse rapidly into the dry atmosphere around. As a result of the presence of this moisture-laden air in the immediate neighbourhood of the leaf-surface, transpiration of water-vapour from the interior through the stomata is retarded. These *covering hairs* are usually dead and, at maturity, occupied only by air; such dead hairs often appear white, showing that a large proportion of the light falling upon them is totally reflected, hence they also afford protection against the heating effect of the sun and against excessive illumination. Hairs thus serve to reduce transpiration and act as a screen to the underlying chloroplasts. An analogy could be drawn with the interior of a woodland, where beneath the trees the air is cool, shady, and damp, just as it is beneath the hairs on a leaf. Not uncommonly hairs are only present on the young leaf, falling off as the latter matures (*e.g.* Plane, Horse Chestnut, etc.).

The simplest type of covering hair is unbranched and usually tapers towards the tip (Fig. 95, B–D). Short stiff hairs of this kind are found in some Boraginaceæ (*e.g.* Forget-me-not, etc.), but they are often much longer, and either interwoven to form a woolly tangle (*e.g.* Coltsfoot, Thistles, young leaves of the Horse Chestnut, etc.) or all disposed in the same direction, giving a silky appearance to the surface of the leaf (*e.g.* Silverweed, *Potentilla anserina*). Long unbranched hairs from the seed-coat of the Cotton-plant (*Gossypium* spp.), a member of the Mallow-family (Malvaceæ), are the source of cotton.[1] They are unicellular and may reach a length of 2–5 centimetres and serve for the dispersal of the seeds by wind. Similar hairs, with the same function, occur on the seeds of the Willow, Willow-herb (*Epilobium*), and many other plants.

The epidermal cells of many petals are drawn out into very short processes, or *papillæ*, which are the cause of the velvety surface and prevent wetting. A similar production of papillæ is not uncommon on the stomatal surface of the leaves of tropical plants growing in damp situations (*e.g.* tropical rain-forest).

Branched hairs assume very diverse forms, only a few of which can be mentioned. In the Mullein and Plane they are tree-like, and consist of an erect multicellular axis from which numerous tapering branches radiate at intervals. More frequent are so-called *stellate hairs*, in which there is but one set of radiating branches terminating a short stalk which, however, is sometimes practically absent (e.g. *Deutzia*). Multicellular hairs of this kind are typical of the Lime-family (Tiliaceæ) and Mallow-family (Malvaceæ), whilst unicellular ones are exemplified in *Deutzia* (Fig. 95, A). Stellate hairs are also found in the Cruciferæ (Fig. 4, C), but here they are accompanied by simpler forms with only two or three branches and by unbranched hairs.

A very efficient transpiration-check is afforded by the *peltate hairs*, which are well seen in the Sea Buckthorn (*Hippophaë*, Fig. 96) and in *Elæagnus*,

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[1] The walls of these hairs are practically pure cellulose. Many hairs, which from their length might be used for the manufacture of textiles, are slightly lignified, and consequently too brittle to spin. Kapok of commerce is obtained from the slightly cuticularised hairs lining the fruit of the Silk-Cotton tree (*Eriodendron anfractuosum*), which is common in the Tropics.

where, owing to the large number of these scale-like structures, the under-surface of the leaf has a characteristic silvery appearance. The short stalk of these hairs is surmounted by a horizontal expansion, consisting of a large number of unicellular rays which are joined together at their base but free at their tips.

Certain climbers (p. 17) are materially aided in clinging to their support by the possession of stiff hairs. Thus the ridges on the stem of the Goosegrass (*Galium aparine*) bear numerous reflexed unicellular hairs, shaped like a hook. In the Hop the ridges are similarly beset by stiff hairs, with two arms situated in the vertical plane, on a small elevation of the epidermis. Extreme types of multicellular climbing hairs are furnished by the prickles of the Rose and Bramble.

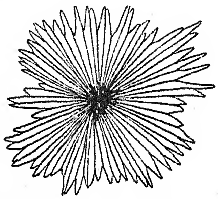


FIG. 96. Peltate hair of Sea Buckthorn (*Hippophaë rhamnoides*).

Whilst the walls of the ordinary covering hairs are generally not appreciably thickened, both branched and unbranched hairs may possess thick walls which are frequently silicified or calcified; when thus stiffened, they constitute a *chevaux-de-frise* against small animals (*e.g.* slugs). Good examples are afforded by the unbranched bristle-hairs of many Boraginaceæ (*e.g.* Borage, Comfrey, etc.) and the branched types found on Stocks and other Cruciferæ. Their effect is often accentuated by the presence of numerous minute teeth on their surface (Fig. 95, A).

One of the most striking examples of hairs acting as a deterrent to animal attacks is, however, furnished by the unicellular *stinging hairs* of the Nettle (*Urtica*) (Fig. 97, D). Each is borne on a multicellular stalk in which is embedded the thin-walled swollen base of the actual stinging hair. The upper part of the latter is comparatively thick-walled and tapers gradually to near the apex, where it suddenly enlarges to form a tiny bead-like tip (Fig. 97, E). The lower part of the wall is calcified, the upper part silicified. The living protoplasmic contents often show distinct streaming movements, and include a large vacuole filled with acrid sap. When an animal brushes against one of these hairs, the little tip breaks off, leaving exposed a fine needle-like point formed by the upper tapering part of the hair. As a result of the pressure of contact, this fine tube penetrates the skin, and the compression of the bladder-like base injects the contained fluid into the wound.

The hairs of many plants produce secretions[1] which are often of the nature of ethereal oils (cf. p. 90). Such *glandular hairs* are

[1] Water- and sugar-secreting hairs are considered in Chapter XVIII.

multicellular and generally consist of a basal cell, which is usually sunk in the epidermis, a projecting stalk, and a glandular head (cf. Fig. 118, *g.h.*), but are otherwise of very diverse form. In the Chinese Primrose (*Primula sinensis*, Fig. 97, A–C) and the Garden Geranium (*Pelargonium*), the head is formed by a single cell and the stalk by a varying number of cells. In the Labiatæ (*e.g.* White Deadnettle) the head is composed of four or more

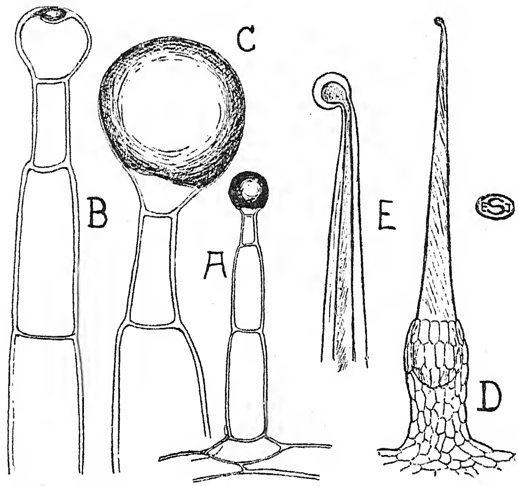


FIG. 97. Glandular hairs of Chinese Primrose (*Primula sinensis*, A–C) and Stinging Hair of Nettle (*Urtica*, D, E). In A–C the secretion is shaded, and in C and E only the greatly magnified tip of the hair is shown.

cells disposed in a plane parallel to the surface of the leaf. Extended division of the head leads to the peltate type of glandular hair, such as is seen in the Hop (Fig. 95, E) and the Black Currant.

All the cells of such glandular hairs are living, those of the head which are concerned in active secretion being specially characterised by dense protoplasmic contents and large nuclei. Small droplets of secretion can often be recognised within the young glandular cells, but in the mature condition the ethereal oil is found deposited between the cuticle and the cellulose-layer of the outer wall (Fig. 97, B), so that after solution of the oil by means of alcohol a space is evident beneath the cuticle. The volatile oils produced by these glands are the cause of the fragrant perfume of many herbs (*e.g.* Lavender).

CHAPTER XV

THE STRUCTURE OF THE LEAF

THE detailed structure of dorsiventral leaves is most easily realised in a transverse section. Beneath the colourless epidermis (Fig. 98, *Ep.*) of the upper side are one or more layers of vertically elongated cells constituting the *palisade tissue* (*Pa.*), which is especially concerned with photosynthesis; its cells are deep green owing to the numerous chloroplasts. Between the palisade layer and the lower epidermis lies the loose "*spongy*" *tissue* (*Sp.*), which is composed of irregular cells separated by many and often conspicuous intercellular spaces (*In.*). This tissue contains fewer chloroplasts and communicates with the external atmosphere by way of the stomata. Palisade and spongy tissues together constitute the ground-tissue, or *mesophyll*, of the leaf. Here and there the section will pass through *veins*, some cut transversely, others obliquely or longitudinally; the veins include the vascular tissue with xylem towards the upper and phloem towards the lower side, and each is surrounded by a well-defined layer of cells, the *bundle-sheath* (*Sh.*).

Good material for a detailed study is furnished by the *Fuchsia*. The features of the epidermis have been fully described. The *palisade* cells are four to six times as long as broad and form a single layer (Fig. 98, *Pa.*). They are attached on the one hand to the upper epidermis, and on the other to the rounded cells constituting the uppermost layer of the spongy parenchyma. Narrow intercellular spaces, extending the whole depth of the palisade layer, occur at intervals between the cells, but these spaces are only apparent here and there in the transverse section (cf. Fig. 98, *Pa.*). In sections parallel to the surface of the leaf the palisade cells appear rounded (being cut transversely, Fig. 99, A), so that they have the form of a number of closely packed cylinders placed side by side and interspersed with regularly disposed vertical spaces (*i.p.*), where the curved surfaces are not in contact.

The numerous lenticular *chloroplasts* form an almost continuous

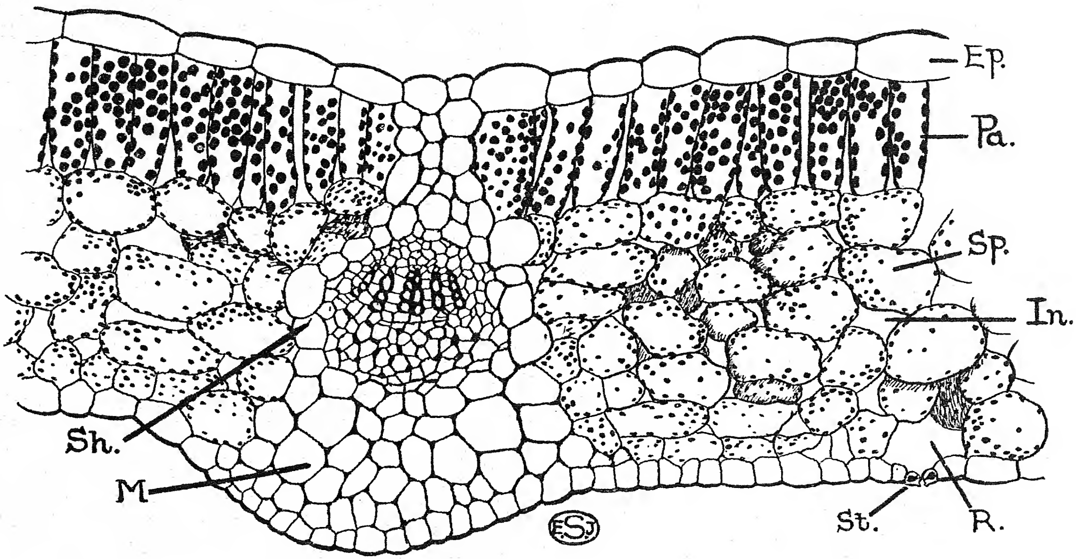


FIG. 98. Transverse section of the leaf of *Fuchsia* passing through a vein. *Ep.*, epidermis; *In.*, intercellular space; *M.*, collenchyma of the midrib; *Pa.*, palisade layer; *R.*, respiratory cavity; *Sh.*, sheath of vascular bundle; *Sp.*, spongy parenchyma; *St.*, stoma.

layer in the cytoplasm lining the vertical walls, a feature well seen in both transverse and surface sections (Fig. 98, *Pa.*; Fig. 99, A; see also Fig. 89). This peripheral position is clearly favourable to the rapid absorption of carbon dioxide from the adjacent intercellular spaces. Moreover, the chloroplasts, as a result, present their edges to the light so that the chlorophyll is protected from the injurious effects of excessive illumination. Owing to the considerable length of the palisade cells, there is accommodation for a large number of chloroplasts in each. In some plants,

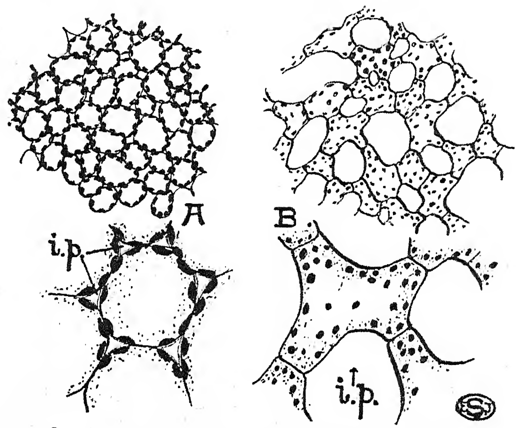


Fig. 99. Sections parallel to the surfaces of a *Fuchsia* leaf, cut respectively through the palisade layer (A) and through the spongy parenchyma (B). In each the lower figure shows a small portion on an enlarged scale. *i.p.*, intercellular spaces.

however, the chloroplast-bearing surface is increased by the development of special infoldings of the wall [*arm-palisade, e.g.* in the leaves of the Elder (Fig. 100, *a.p.*)].

In the transverse section of the leaf of the *Fuchsia* two or three palisade cells frequently join by their lower ends on to one and the same cell of the spongy parenchyma (Fig. 98; see also Fig. 100, *c.c.*; Fig. 346). The cells in question are usually broadened at their upper ends, so that they are more or less funnel-shaped. Presumably the photosynthetic products (carbohydrates, etc.) formed in the palisade cells pass into these *collecting cells* and from them diffuse, via other spongy elements, to the veins.

The *spongy parenchyma*, in its most typical form (*e.g.* in *Euphorbia amygdaloides*), consists of irregularly lobed cells attached to one another by their projecting arms (cf. Fig. 346), so that wide intercellular spaces occur between them. In the *Fuchsia* and in many leaves, however, the cells are more rounded and the inter-

spaces consequently smaller (Fig. 98, *In.*; Fig. 99, B). The rather few chloroplasts in the spongy, as compared with the palisade, parenchyma may be related to the fact that the former tissue receives relatively little light. The layer in contact with the lower epidermis is not uncommonly continuous (except for the gaps constituted by the respiratory cavities, Fig. 98, *R.*), and its cells may even show a palisade-like form when they generally contain rather numerous chloroplasts (*e.g.* Corn Cockle), and serve to utilise the light reaching the under side of the leaf.

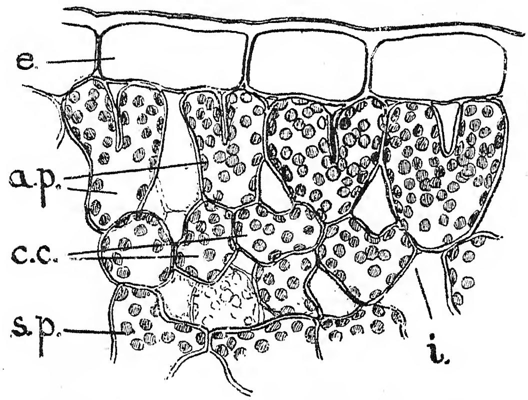


FIG. 100. Transverse section through part of the leaf of the Elder (*Sambucus*) showing the upper epidermis (*e.*); the arm-palisade cells (*a.p.*); the collecting cells (*c.c.*); and the spongy parenchyma (*s.p.*). *i.*, intercellular space.

The spongy tissue creates an extensive intercellular system communicating on the one hand with the external atmosphere by way of the stomata, and on the other hand with the entire aerating system of the rest of the plant. The spongy cells also serve to conduct elaborated food-materials in various directions to the adjacent veins, whilst their cell-sap provides a reserve supply of water which may be partially surrendered to the palisade cells, with their higher suction force.

The structure of the mesophyll just described is characteristic of *dorsiventral leaves* generally, the following being the chief modifications. The palisade tissue not uncommonly consists of several layers (*e.g.* Holly, Fig. 89, A), a feature especially encountered in leaves exposed to strong illumination, whilst leaves developed in dull light may have little or no palisade tissue. In some plants (*e.g.* the House-leek) the photosynthetic cells are elongated parallel to the midrib, whilst in transverse section they appear more or less rounded.

Variegated leaves usually exhibit a similar structure to that of the normal foliage of the same species, except that the pale areas lack chlorophyll and may have smaller epidermal cells. It need hardly be said that the structure of reduced foliage-leaves (*e.g.* scale-leaves of rhizomes, bud-scales, etc.) is of a much simpler character. Such are usually colourless with a homogeneous mesophyll, and often possess no veins.

Movement of chloroplasts in conformity with the intensity of illumination is seen in a few plants (*e.g.* Duckweed, *Lemna*; Moss-leaves, etc.). In these the chloroplasts occupy a profile position on the vertical walls when the light is intense, whilst when weak the chloroplasts pass to the horizontal walls, so that their full surface is presented towards the source of illumination.

The *vascular tissue* of the leaf is very extensive, forming a network in Dicotyledons and a parallel system in most Monocotyledons.[1] The repeated branching facilitates not only the delivery of water and mineral salts to all parts of the leaf, but also the rapid removal of elaborated food-substances. The vascular system, however, also constitutes a supporting skeleton for the lamina, in which it is often aided by accompanying mechanical tissues; the latter are found especially in the larger veins, and consist of strands of collenchyma (Fig. 98, *M.*) or sclerenchyma, which run both above and below the vascular bundles or sometimes on the lower side only.

A transverse section through one of the principal veins of the leaf shows a single bundle enveloped in a sheath of one or more layers of large transparent thin-walled parenchyma-cells (Fig. 98, *Sh.*; cf. also Fig. 346, *V.*); the accompanying collenchyma (*M.*) is developed especially on the lower side. The xylem, which is adjacent to the palisade tissue, consists of rows of vessels alternating with wood-parenchyma, the protoxylem being directed towards the upper epidermis; the phloem is of the normal type and lies towards the lower side. Between xylem and phloem a cambium can often be recognised (Fig. 98), especially in evergreen leaves (*e.g.* Holly) which remain on the plant for more than one year. In the midrib of *Fuchsia* the bundle is bicollateral.

In passing to the finer and finer ramifications of the vascular system a gradual simplification in structure is apparent. The differentiation of the phloem becomes less and less distinct, its place being taken by a more or less uniform tissue of thin-walled elongated cells, whilst at the ultimate terminations of the bundles it often disappears completely. Similarly the xylem-vessels gradually give place to relatively short spiral or reticulate tracheids (Fig. 41, A,

[1] The Cuckoo-pint (*Arum maculatum*) and Black Bryony (*Tamus communis*), for instance, have a venation similar to that of Dicotyledons.

p. 69), the amount of wood-parenchyma diminishing till it dies out. Thus the *bundle-ends* usually consist only of tracheids surrounded by the single-layered parenchyma-sheath.

In larger leaves (*e.g.* Sunflower) the *midrib* often contains several bundles, and in the Docks (*Rumex*) and the Rhubarb (*Rheum rhaponticum*) quite a large number of strands occur. On the whole the vascular supply is proportional to the size of the leaf, and this is

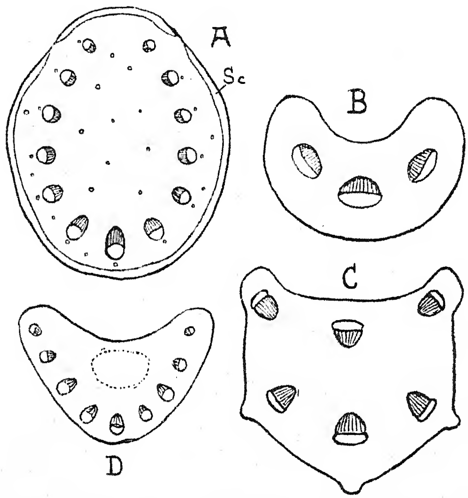


FIG. 101. Diagrams showing the petiolar structure of A, Sea Holly (*Eryngium maritimum*); B, Dog's Mercury (*Mercurialis perennis*); C, Black Bindweed (*Polygonum convolvulus*); D, Bishop's Weed (*Ægopodium podagraria*). The shaded part of the bundles represents xylem, the unshaded part phloem. *Sc.*, sclerenchyma.

true also of that of the *petiole*. In small leaves (e.g. *Cerastium*, Fig. 102) the latter frequently contains but a single vascular strand orientated as in the lamina, whilst in larger ones there are several bundles usually grouped in the form of a *C* with the opening towards the concave or flattened upper surface and with the protoxylems directed inwards (Fig. 101, A–D). Sometimes the petiolar strands form a complete ring, and the individual bundles may depart from the normal form. The part of the ground-tissue included within the group of strands is spoken of as pith, and that outside as cortex, the peripheral layers of the latter not uncommonly consisting of mechanical tissue (Fig. 101, *Sc.*).

The bundles of the petiole can be traced backwards some little distance into the cortex of the stem, following a slightly oblique course, so that, in sections cut transversely just below the nodes, the

one or more bundles (*leaf-trace bundles*) passing from the leaf into the stem appear cut obliquely in the cortex. After penetrating some little way into the latter the bundles turn abruptly downwards and run vertically through one or more internodes, ultimately, with (Fig. 102) or without previous branching, fusing laterally with strands derived from other leaves. The bundles traversing the stem are therefore merely downward continuations of those found in the leaves. In the region of the nodes the vascular system may be very complex and not uncommonly forms a more or less continuous network of vessels or tracheids with diverse orientation. The vascular supply of the axillary bud often arises from the central cylinder as two separate strands which soon unite to form a ring (cf. Fig. 115, p. 191). The vascular supply of stipules originates from the leaf-trace strands.

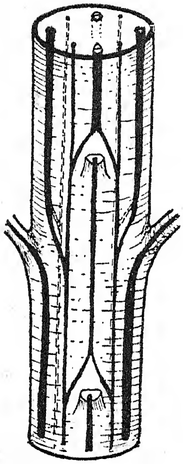


FIG. 102. Diagrammatic representation of the vascular system in a small portion of the stem of *Cerastium* (modified from Prantl). Only the bases of the leaves, with a single vascular strand, are shown.

In Monocotyledons the sheathing leaf-bases completely encircle the axis, numerous strands passing from each leaf into the stem. The median vascular bundles often pass almost to the centre of the stem before they bend downwards; subsequently they pursue a longitudinal direction, at the same time returning obliquely towards the periphery. The more laterally placed strands follow a similar course, but do not penetrate to the same depth. As a result the vascular bundles from the successive leaves usually appear irregularly scattered through the cross-section (cf. p. 140), but tend to be more densely crowded near the outside (Fig. 87, D, p. 145).

The mechanics of the leaf differ in several respects from that of the stem. The petioles of most leaves, when at rest, have to withstand a one-sided strain acting mainly from above and due to the weight of the blade, which may be much increased during rain. The arrangement of the mechanical tissue in the form of an inverted arch, open on the upper side (see Fig. 101, B, D), gives considerable strength to meet the usual bending strains from above, but is not so rigid as the closed tube found in stems. It therefore allows of a certain flexibility, so that the leaf readily assumes a streamline position during gusts of wind. In such leaves as the Sycamore (Fig. 72), Wood-sorrel (Fig. 173), and Garden Nasturtium (Fig. 117, B), in which the petiole is attached

more or less centrally and at right angles to the blade, the strain is almost equally distributed over the leaf-stalk and the arrangement of the vascular strands is more like that of a stem (cf. Fig. 101, C). In radical leaves (*e.g.* Daisy) which rest on the ground, the open arch arrangement is greatly flattened out.

The tearing action of wind and hail is to a large extent obviated by the strengthening network formed by the veins, and especially by the occurrence of marginal mechanical elements. The latter either form arched connections running parallel to the leaf margin, between the finer vascular strands (*e.g.* Red Currant) or bundles of fibres (e.g. *Iris*) occupying the same position. Moreover, the epidermal cells at the edge of the leaf are usually especially thickened and have a pronounced cuticle.

The leaves so far considered exhibit a marked difference of structure and appearance between the upper and lower surfaces (dorsiventral type), which is probably related to the horizontal position. In the *Iris* and other Monocotyledons, where the leaf-blades stand vertically and both surfaces receive an equal amount of light, the structure is identical on the two sides (isobilateral type). In still others (*e.g.* Onion, White Stonecrop, *Sedum album*), the leaves are more or less cylindrical, and, apart from the dorsiventral arrangement of the vascular bundles, exhibit radial organisation, with a palisade layer extending uniformly round the periphery (centric type).

CHAPTER XVI

SECONDARY THICKENING

It was pointed out in the preceding chapter that the vascular supply of the leaf is roughly proportional to its size (p. 167), and in the same way the vascular system of the stem is correlated with the area of leaf-surface which it bears. With the annual increase of foliage exhibited by all woody perennials, a need for additional conducting elements arises, and this want is supplied through the activity of a meristem (the cambium, p. 136) situated between the xylem and phloem of the bundles. *Cambium* is found in this position in all Dicotyledons and Conifers (see p. 412), but in Monocotyledons is present only occasionally as a vestige (*e.g.* in the leaf-sheaths of the Maize and in the leaves of many other Grasses). The division of the cells of the cambium leads to the formation of additional conducting elements, accompanied by a gradual increase in the size of the stem, spoken of as *secondary thickening*. Enlargement does not, however, always imply cell-division, since in some Palms, where no active cambium occurs, there is increase in girth mainly due to enlargement of the cells already present.

The cambium may be regarded as arising from an unaltered remnant of the procambium (cf. p. 147), which has retained its powers of division, but until it becomes active it is difficult to recognise. The actual cambium is established by the appearance of two parallel tangential walls in the persisting procambial elements. There is thus cut out a single layer of radially flattened cells (Fig. 103, *C.*) which have dense protoplasmic contents and prominent nuclei and, as seen in longitudinal section (cf. Fig. 84, *Ca.*, p. 140), have an elongated form and tapering ends. Subsequent division of these cells takes place parallel to the two tangential faces whereby files of segments are produced, both on the outer and inner side, those adjacent to the phloem becoming differentiated as additional (secondary) phloem, those adjacent to the xylem as additional (secondary) xylem. In certain sectors, however, the cambium consists of isodiametric cells, forming

spindle-shaped groups in tangential section; from these the rays (p. 173) are produced.

According to the character of the procambial tissue (cf. pp. 146, 147), the cambium at first consists either of separate strips which subsequently join laterally, or it appears as a complete cylinder from its inception. In the former case, subsequent to the

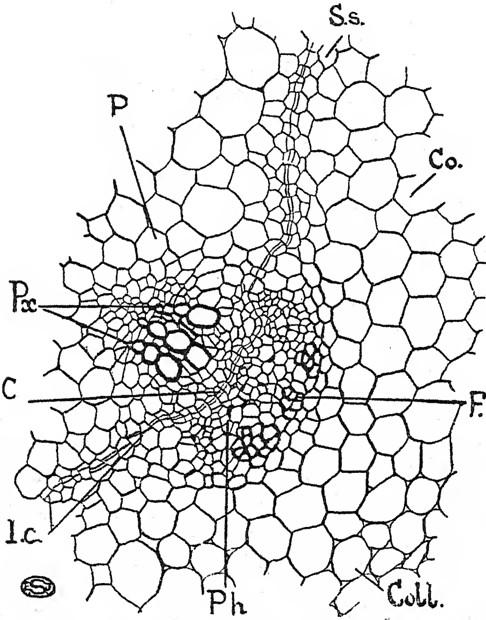


FIG. 103. Transverse section of a small portion of the hypocotyl of the Castor Oil plant (*Ricinus communis*). *C.*, intrafascicular cambium; *Co.*, cortex; *Coll.*, collenchyma; *F.*, pericyclic fibres; *I.c.*, interfascicular cambium; *P.*, parenchyma; *Ph.*, phloem; *Px.*, protoxylem; *S.s.*, starch sheath.

development of the cambium within the bundles, a similar division by two tangential walls takes place in certain cells of the rays, and, where a starch-sheath is present, these occur in the pericycle (*e.g.* hypocotyl of the Castor Oil plant, Fig. 103, *I.c.*). The cambium between the bundles (*interfascicular*, Fig. 103, *I.c.*) links up with that within the bundles (*intrafascicular*, Fig. 103, *C.*) to form a complete meristematic ring. In woody perennials the cambium resumes its function each year, although division is arrested during the winter months.

The secondary wood thus added on the inside forms a larger and larger core each year (Fig. 104). Since it is composed of hard

persistent tissue, there is practically no compression of the wood, which progressively augments, so that the increase in girth of the stem serves as a rough measure of the amount of tissue added. To this enlargement the secondary phloem contributes but little, since this tissue is mainly thin-walled, and the outer earlier-formed elements become compressed more and more, as a consequence

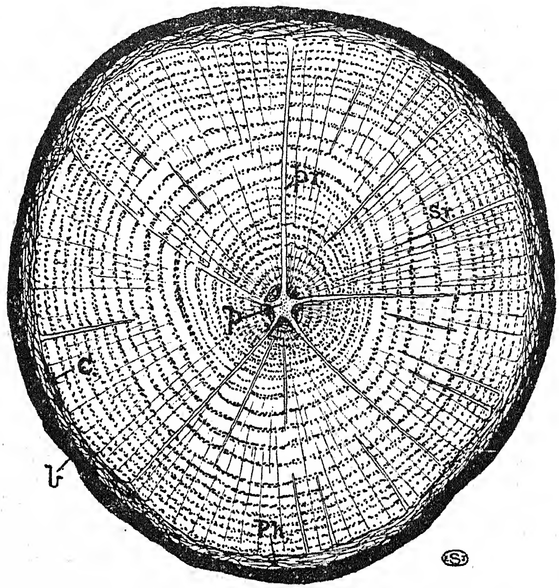


FIG. 104. Diagram showing the arrangement of tissues in a transverse section of a woody trunk, about twenty-four years old. The large vessels of the spring wood of each annual ring are shown as black dots. *b.*, bark; *c.*, region of cambium; *p.*, pith; *Ph.*, secondary phloem; *pr.*, primary ray; *Sr.*, secondary ray.

of the increasing pressure resulting from the growth of the wood and the annual formation of intercalated phloem. The cambium keeps pace with the enlarging circumference of the secondary wood, mainly by radial division and growth of its cells or by transverse divisions and gliding growth (p. 59).

The pressure on the outer tissues, due to the *interpolation of secondary vascular elements* between the primary xylem and phloem, becomes more and more marked as the years go by and its effects are most pronounced in the cortex. Moreover, the steady increase in size of the woody core results in a gradual enlargement of its circumference, so that the softer tissues beyond become tangentially stretched. This tension can be readily

demonstrated by making an extended vertical incision through the cortex of a three-year-old twig of the Ash. The edges of the cut are seen to separate immediately owing to transverse contraction of the thin-walled tissues. In nature the tangential tension is exemplified by the irregular longitudinal fissures which are so marked a feature of the older bark of many trees.

In regions where the cambium consists of groups of isodiametric cells (p. 170), the segments cut off are parenchymatous, and differ from the other elements of the wood and phloem in being radially and not longitudinally elongated (Fig. 106, A, *m.r.*). In transverse sections of a secondarily thickened stem these *parenchyma rays* appear as a number of radiating streaks, one or more cells in width (Fig. 104, *pr.* and *Sr.*). Some of these rays extend from cortex to pith (*pr.*) and, since they correspond in position to the original rays between the vascular bundles, are called *primary* rays; others (the *secondary* parenchyma rays, *Sr.*), however, though traversing the greater part of the secondary phloem, penetrate only to a varying depth towards the centre. In some plants (e.g. *Aristolochia*) the primary rays are very wide, and practically the whole of the interfascicular cambial strips participate in their formation.

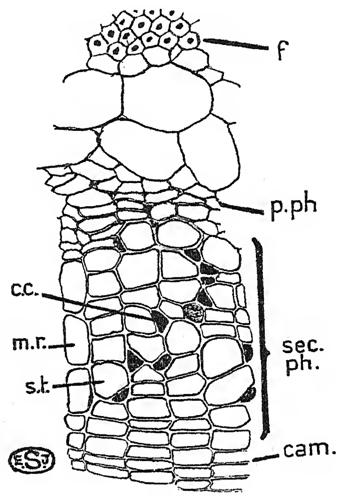


FIG. 105. Transverse section of the outer part of the stem of the Horse Chestnut (*Æsculus*), showing the secondary phloem (*Sec. ph.*) and the cambium (*Cam.*). *c.c.*, companion cells; *f*, fibres of pericycle; *M.r.*, parenchyma ray; *P.ph.*, primary phloem; *s.t.*, sieve-tube.

The *secondary wood* is composed of four main types of elements, viz. vessels, tracheids, wood-fibres, and wood-parenchyma, but transitions between the different types are not infrequent. The component elements often exhibit a distinct radial arrangement (*e.g.* Horse Chestnut), though this may be somewhat obscured when the vessels are large and numerous (*e.g.* Lime, Elm). The *vessels* of the secondary wood usually bear densely crowded bordered pits (Fig. 106, *V*; Fig. 40, E, *b*, p. 68), often arranged in distinct vertical series, and not uncommonly show additional reticulate or spiral thickenings deposited on the inner surface of the wall. The perforated septa are frequently oblique (Fig. 106, C, *V*) with reference to the radial plane, a

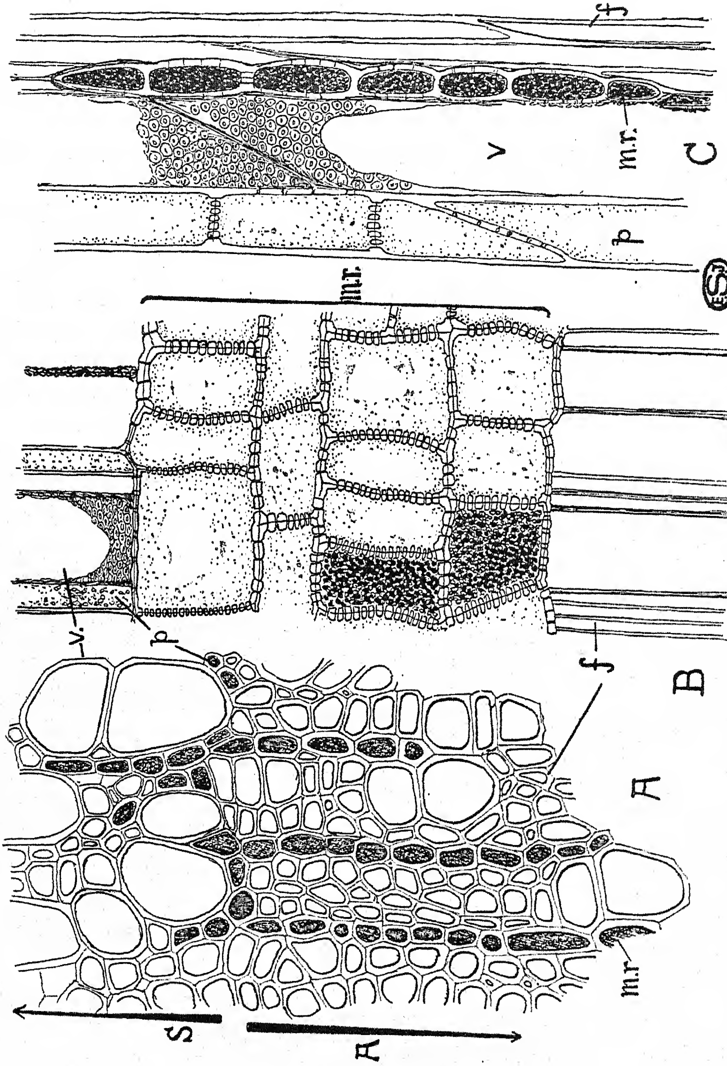


FIG. 106. Structure of the secondary wood of the Horse Chestnut (*Æsculus*). A, Transverse section showing the spring-wood (*S.*) of one, and the summer-wood (*A.*) of the preceding annual ring. *B*, Radial longitudinal section. C, Tangential longitudinal section. *f*, fibres; *m.r.*, parenchyma rays; *p*, wood-parenchyma; *V*, pitted vessels of secondary xylem.

feature which can be related to the peculiar form of the cambial segments from which the vessels are derived. The perforations are varied (cf. p. 61 and Fig. 40, D–F), but the type in which a number of cross-bars remain is commoner than in the primary wood. *Tracheids* (cf. p. 70) differ from vessels in being derived from single segments of the cambium, which show no open perforations in the end-walls; they are usually much shorter than the vessels, but of about the same width. The vessels and tracheids are the water-conducting elements of the secondary wood, and the former are generally much more numerous than the latter; in fact, tracheids may be almost absent (*e.g.* Willow).

The typical *wood-fibres* closely resemble those described on p. 66, having pointed ends and more or less thickened walls, which are provided with oblique slit-shaped simple pits (Fig. 106, *f.*). As the pit-apertures on the two sides of the wall are often inclined in opposite directions, a X-like appearance is commonly presented. Fibres of this type are connected by transitions with others which bear bordered pits with oblique slits (*e.g.* Beech), and differ but little from the fibrous tracheids of the Conifers (see p. 412). In the typical wood-fibres the walls are lignified and the contents dead; but fibre-like cells with living protoplasts occur in the secondary wood of the Sycamore and of many herbs. Such fibres are occasionally septate (*e.g.* Vine) and constitute transitions to wood-parenchyma. Where vessels are in contact with the ordinary mechanical fibres, pits are not developed on the walls.

The *wood-parenchyma* cells of the secondary xylem resemble those of the primary xylem, in form and in the possession of a living protoplast; the walls are, however, commonly thicker and often lignified, the horizontal ones showing prominent pitting (Fig. 106, *p.*). Wood-parenchyma cells may be generally distributed throughout the wood (*e.g.* Birch, Beech), or more especially confined to the summer-formed wood and the immediate vicinity of the vessels, sometimes completely ensheathing them (*e.g.* Ash). The parenchyma in contact with the vessels bears simple pits corresponding in position to pits of the vessel wall, which latter are here either simple (*e.g.* Oak) or bordered (*one-sided bordered pits*), like the remaining pits of the vessel wall.

The structure of the *parenchyma rays* can only be fully appreciated by a study of their appearance in transverse and in longitudinal sections, both radial and tangential. In the transverse section the cells, except for the fact that their long axis is placed radially and not vertically, are very similar to those of the wood-parenchyma, though not uncommonly having somewhat thinner walls. The latter bear simple pits which are often particularly

numerous on the tangential walls (Fig. 106, B; Fig. 108, *m.*). The simple pits of the radial walls and the bordered pits of the vessels combine to form one-sided bordered pits like those described above.

Attention has already been drawn to the variable width of the rays. In general the secondary parenchyma rays are narrow and often only one cell wide; the primary ones in most trees do not greatly exceed the secondary in width, but in many herbs the contrast is extremely marked. Each ray is a plate of cells of which the full vertical extent is seen in tangential longitudinal sections (Fig. 106, C, *m.r.*). The secondary parenchyma rays are very limited in this direction, rarely exceeding ten or twelve cells in height, whilst the primary rays usually extend through an entire internode. Each ray, as seen in tangential section, is somewhat spindle-shaped as a result of the tapering of the cells at the upper and lower margins (Fig. 106, C, *m.r.*).

In radial longitudinal sections the secondary rays are cut parallel to their flat faces, and appear as so many narrow parenchymatous strips passing at right angles across the longitudinal grain of the wood (Fig. 106, B). The detailed structure of the ray here somewhat resembles that of a brick wall, the alternation of the cells simulating the "bond" of the bricks. The component cells show plainly the radial elongation referred to above, but sometimes those at the upper and lower margins are short and not markedly lengthened (*e.g.* Willows). The radial, like the vertical, extent of the secondary rays is seen to be limited (cf. p. 173). Should the radial section pass through one of the primary rays, the latter will be seen to show a far greater development, both in the vertical and radial directions.

Apart from the occasional presence of fibres with protoplasmic contents, the wood-parenchyma and the parenchyma rays are the only living constituents of the secondary wood. The living cylinder constituted by the phloem and cortex is thus connected with numerous inwardly directed plates of living tissue, the parenchyma rays. Of these, however, only the primary ones extend to the pith, where they are linked up by a second cylinder of living cells, the *medullary sheath* (p. 137), which invests the inner margins of the primary xylem strands. The radiating plates formed by the secondary rays are, however, not isolated, even where they pass between the dead elements of the secondary wood, since they are connected both vertically and horizontally by bands of wood-parenchyma cells.

The mass of vessels and fibres is thus permeated by a continuous system of living elements connected with the food-conduct-

ing tissues. The functions of this system are twofold: firstly, to conduct elaborated food-substances to the cambial region, the living cells of the wood, and the medullary sheath; secondly, at certain times of the year, the cells serve for the *storage* of food-substances, *e.g.* starch, as can be shown by the application of iodine to a section of a twig in autumn. When this starch is utilised during the sprouting of the buds in spring, it is changed into sugar, and is then transferred in the water ascending the vessels to the growing regions, hence the sweet character of the sap which exudes in bleeding.[1] The aeration of the secondary tissues is effected by narrow intercellular spaces which are more particularly associated with the living elements.

The major part of each annual addition to the secondary wood usually consists of vessels and fibres, but the proportion of these latter varies with the kind of plant and during each season's growth. The wood formed in the spring (*spring-wood*, Fig. 106, A, *S.*) mostly contains a much larger percentage of vessels than that produced later (*summer-wood*, *A.*); its vessels, moreover, are often larger and have thinner walls, and the same may be true of the fibres. This difference can be related to the sudden demand on the water-supply in the spring on the part of the newly-expanding leaves, whilst later in the season provision can be made for the growing mechanical requirements[2] of the plant by an increased proportion of fibres. As a consequence there is often a sharp boundary between the dense small-celled summer-wood of one season and the wide-celled spring-wood of the next (Fig. 106), and this leads to the marking out of the secondary wood into a succession of *annual rings* (Fig. 104), by means of which the approximate age of a trunk can be estimated. In Evergreens and some other trees in which the seasonal leaf-production is not so marked, the vessels tend to be more evenly distributed. Such wood is termed *diffuse-porous*, in contrast to the *ring-porous* type previously described.

Occasionally, when a new set of leaves is produced to replace a first crop killed by frost or devoured by caterpillars, their expansion is accompanied by the formation of a second zone of spring-wood, so that two "annual rings" are formed in a single season. The width of the annual ring is mainly determined by nutrition, often influenced by climate, though the variations in thickness in one and the same ring are probably the result of mechanical strain.

[1] Cf. pp. 84, 194. Maple-sugar is derived from the evaporated sap of *Acer saccharinum* (North America), obtained by tapping the trees in spring.

[2] A feature that is probably also connected with the growing mechanical strain is the increased length of the fibres in the later-formed annual rings.

Such asymmetrical annual rings, with a maximum development on the upper or lower side, are commonly found in horizontal branches. Extreme asymmetry is seen in the "buttress-roots" observed in many tropical trees (*e.g.* species of *Ficus*).

The constant addition of new wood is probably mainly necessitated by changes in the central earlier-formed xylem, as a result of which it becomes useless for purposes of conduction, although such changes often increase its value as a mechanical support; it is then spoken of as *heart-wood* in contrast to the active *sap-wood* beyond. The elements of the heart-wood often become impregnated with tannins, resins, etc., which are frequently accompanied by dark-coloured pigments; in some trees the latter are extracted and afford useful dyes, *e.g.* the logwood (hæmatoxylin) obtained from *Hæmatoxylon campechianum* (Tropical America). The employment of mahogany, walnut, etc., in cabinet-work is largely due to the rich colouration of the heart-wood and the high polish which its hard character enables it to take. In the Ebony-tree (*Diospyros*) the living sap-wood is white and even soft, the ebony of commerce being the mature, very hard, and jet-black heart-wood. In some plants (*e.g.* Beech) little heart-wood is formed, most of the xylem remaining functional.

The impregnating substances are often antiseptic, and prevent decay by inhibiting the development of Fungi and Bacteria, thus increasing the durability of the wood. Teak (*Tectona grandis*) owes its great value as a tropical timber to the presence of an oil which renders it immune from the depredations of wood-boring insects; it is also the cause of its peculiar scent. The liability of many Willows to develop hollow trunks at an early stage may be attributed to the absence of antiseptic substances from the older wood.

The cavities of the water-conducting elements in the heart-wood are frequently blocked in various ways, most commonly by the ingrowth of structures known as *tyloses* (Fig. 107). These are bladder-like intrusions through the pits, from the wood-parenchyma cells, into the vessels, and are sometimes so numerous as to fill the latter completely with a false tissue resembling parenchyma. They are bounded by the extended thin-walled pit-membrane, which undergoes a certain amount of surface growth, and occasionally becomes thickened and lignified (e.g. *Robinia pseudacacia*). Each of the young tyloses is living, containing cytoplasm, cell-sap, and sometimes also a nucleus; but when they have reached their full size both the tyloses and the wood-parenchyma cells [1] of the heart-

[1] The latter are invariably dead in the mature heart-wood, even when no tyloses are formed.

wood die, so that the whole of the latter consists of dead elements. Tyloses are also produced in herbaceous stems (*e.g.* Vegetable Marrow, Fig. 107), but here their function is obscure. The plugging of the vessels of the heart-wood is, however, not always effected in this way, since in other plants mineral deposits (lime in the Elm) may take their place.

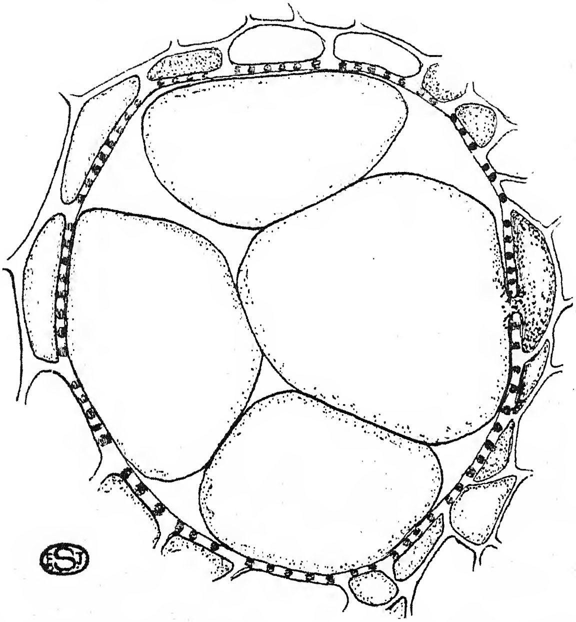


FIG. 107. Tyloses in a vessel of the Vegetable Marrow (*Cucurbita*) as seen in transverse section. On the right the connection with the wood-parenchyma is shown.

In tree-trunks, which have been cut across, the vessels look like small pin-pricks on the smooth surface of the wood and the annual rings are often clearly recognisable. Traversing the cross-section like the spokes of a wheel are the rays. If we examine a block of wood which has been cut radially, we can recognise the long tubes formed by the vessels and irregularly shaped silvery bands passing across them (the silver grain of the Oak), which are the rays. When the wood is cut tangentially, the same features may be made out, the rays now, however, appearing as short vertical streaks.

The mechanical properties of *timbers* [1] depend largely on the proportion of fibres, on the number and size of the vessels, and on the thickness of the

[1] Further details will be found in: A. L. Howard, *A Manual of Timbers of the World*. Macmillan & Co., 2nd edit., 1934 (672 pp.).

fibre walls. Thus, so-called close-grained woods (*e.g.* Box, Holly, etc.) are characterised by having abundant fibres and small vessels, whilst the coarse or open grain of wood (seen in the Lime, Horse Chestnut, etc.) is due to the large number of wide vessels and often to the thin character of the fibres as well. The "soft woods" of commerce are mostly obtained from Conifers whose wood is solely composed of long narrow tracheids (cf. p. 412), having thinner walls than the fibres of hard-wood trees.

The employment of timber for commercial purposes is determined by such qualities as closeness of grain, ease of working, elasticity, toughness,

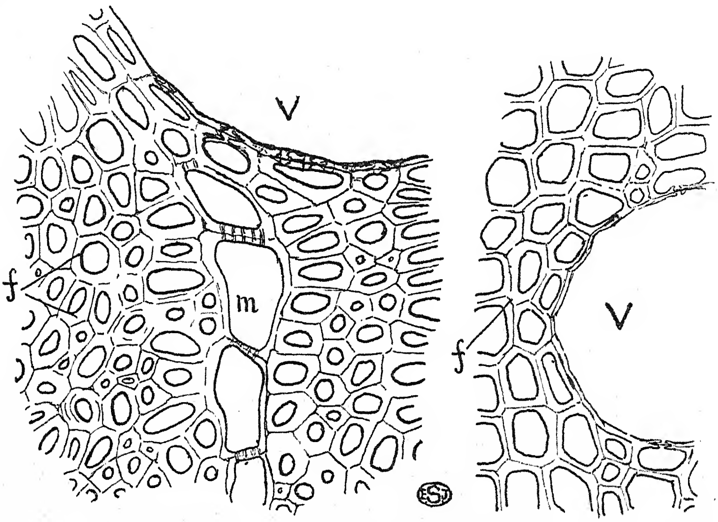


FIG. 108. Transverse sections of the secondary wood of the Sycamore (*Acer pseudoplatanus*) (right) and the Oak (*Quercus*) (left). Note the fibres (*f*), which are much thicker-walled in the latter than in the former. *m*, parenchyma ray; *V*, vessels.

durability, colour, figure, etc. Thus the resilience of the wood of certain types of Willow is responsible for their use in the manufacture of cricket-bats, whilst the ancient esteem of Yew (*Taxus baccata*) for bows, and the modern use of Ash for aeroplane-construction, are the outcome of the elasticity and toughness of these woods. The elastic limit of Ash is only reached under a strain of about 5000 lb. per square inch as compared with 3500 lb. for Douglas Fir. Such qualities are probably not only the result of length of fibre, but also one of physical or chemical constitution of the xylem walls. Liability to splitting is often due to a large size of the constituent elements, and it is the reverse condition which renders the timber of the Hornbeam (*Carpinus*) so suitable for cog-wheels, etc. The "figure" of timber, to which many woods owe their value in cabinet-work, is dependent on the direction of the fibres and the prominence of the parenchyma rays when cut in certain planes.

To render timber suitable for use, the cut log needs to undergo a process of *seasoning*, which involves the drying out of the sap and water, a process that in the open occupies from six months to a year or even longer in the case of hard woods, and about half the time for Coniferous timber. Artificial means

(*e.g.* heating in special sheds or by electricity) are now frequently employed in order to shorten this period. The greatest care is necessary in seasoning to avoid undue stresses and strains, which bring about warping and splitting of the timber, defects that commonly develop if the process be unduly hastened. This is mainly due to the fact that the tangential shrinkage is often nearly double that of the radial. For this reason radial cracks, that open wider and wider as the trunk dries, are not uncommon.

Other common defects are the "*knots*," which are constituted by the vascular tissues of lateral branches that have become embedded in the wood of the trunk; in forestry their development is checked by dense planting.

In the following list are enumerated some of the more important timbers and the trees from which they are derived:—

A. Coniferous.

Douglas Fir or Oregon Pine	*Pseudotsuga douglasii* (Rocky Mts.) (constructional work).[1]
Larch	*Larix europæa* (Europe) (sleepers, pit-props, etc.).
Pitch Pine	*Pinus palustris* (United States) (constructional work).
Red Deal	*Pinus sylvestris* (Britain and Scandinavia) (building work, paving blocks, and sleepers).
White Deal	*Picea excelsa* (Norway) (paper-pulp, floor-boards, etc.).
White Pine	*Abies pectinata* (S. Europe) (joinery).
White or Yellow Pine	*Pinus strobus* (N. America) (joinery).

B. Dicotyledonous.

Ash	*Fraxinus excelsior* (Europe) (wheelwright's work, tool-handles, aeroplanes, etc.).
Beech	*Fagus sylvatica* (Europe) (furniture and tools).
Birch	*Betula* spp. (N. Europe, America) (furniture, cabinet-work, bobbins, plywood, etc.).
Black Walnut	*Juglans nigra* (N. America) (furniture).
Blue Gum	*Eucalyptus globulus* (Australia) (constructional work, piers).
Cedar Wood	*Cedrela* spp. (Tropics) (cigar-boxes).
Chestnut	*Castanea vulgaris* (Europe) (constructional work).
Elm	*Ulmus* spp. (Europe, N. America) (coffin-boards).
Hickory	*Carya* spp. (N. America) (shafts, spokes, etc.).
Jarrah	*Eucalyptus marginata* (W. Australia) (constructional work, wood-paving blocks, etc.).
Lignum vitæ	*Guaiacum officinale* (America) (shaft-bearings, etc.).
Lime	*Tilia* spp. (Europe and N. America) (carvings).
Mahogany	*Swietenia mahogoni* (Tropical America) (cabinet-work).
Maple	*Acer* spp. (Europe and N. America) (textile rollers).
Oak	*Quercus* spp. (Europe and America) (numerous uses).
Poplar	*Populus* spp. (Europe, America) (packing-cases, matches, etc.).
Sandalwood	*Santalum album* (Indo-Malaya) (cabinet-work).
Satinwood	*Chloroxylon swietenia* (E. Indies) (cabinet-work).
Teak	*Tectona grandis* (Indo-Malaya) (constructional work).

The *secondary phloem*, like the primary, is composed of phloem-parenchyma, sieve-tubes, and companion cells, but these last are commonly larger and fibres are often present. The septa in the sieve-tubes are not uncommonly oblique and provided with several

[1] A few only of the more important uses are mentioned for each timber.

perforated areas separated by bar-like thickenings (*compound sieve-plates*). In some plants the phloem-parenchyma and sieve-tubes, with their companion cells, are produced in such regular sequence as to form alternating tangential bands. The fibres are likewise often disposed in layers separating the zones of thin-walled elements (*e.g.* Lime, Mallow, etc.). Vertical series of phloem-parenchyma cells, occupied by crystals of oxalate of lime, and elongated secretory elements (*e.g.* tannin-sacs, cf. p. 92) are not uncommon. The older secondary phloem of woody plants, which has passed out of use, is not infrequently shed with the bark (p. 190).

The parenchyma rays of the secondary phloem are continuous with those of the xylem and exhibit the same general structure, except that the component cells remain thin-walled. In certain Flowering Plants (*e.g.* Lime, etc.) the outer ends of the primary parenchyma rays exhibit a marked V-shaped enlargement, whereby the secondary phloem becomes divided up into a number of wedge-like groups.

A transverse section of any unthickened Dicotyledonous *root* will show a narrow band of two or three layers of parenchymatous cells between each phloem-group and the adjacent xylem. Prior to the commencement of secondary growth tangential division-walls arise in these cells, leading to the production of a *cambium* (Fig. 56, *ca.*, p. 101) like that of the stem. In this way there originate as many cambial strips (Fig. 109, A, B, *C.*) as there are groups of phloem, and, by the active division of the former, secondary xylem is produced on the inside and secondary phloem on the outside. Differentiation of the cambium is at first confined to the inner surface of each phloem-group, but by slow degrees it extends along the sides of the xylem-arms till finally, by the development of tangential division-walls in the cells of the pericycle opposite the protoxylems, a complete lobed cylinder of cambium is established. Owing to the late development of the cambium opposite the protoxylem-groups, secondary thickening is at first more extensive in the bays, so that the outline of the cambium, at first lobed, gradually becomes circular.

The root soon comes to possess a broad ring of secondary wood and phloem (Fig. 109, C), similar to that of the stem, and, as in the latter, traversed by primary (*P.r.*) and secondary *rays*. The former, which, especially in herbs, often attain a considerable width, are situated along the same radii as, and are equal in number to, the primary xylem-groups (*P.xy.*). When these primary rays are broad and consist only of parenchyma, separate wedges of secondary vascular tissues result. The radial extension of the parenchymatous rays is not so marked as that of the wood, so that

certain diarch roots, after secondary thickening, sometimes exhibit a band-like structure (*e.g.* Nettle). The secondary rays, like those of the stem, are generally narrow.

The vessels and wood-parenchyma of the *secondary wood* of the root are relatively more numerous and more evenly distributed

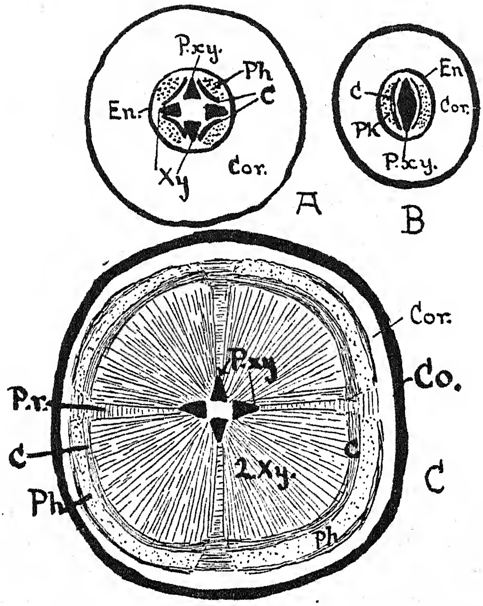


FIG. 109. Diagrams showing secondary thickening in the root. A, a tetrarch, and B, a diarch root, before thickening, showing the position of the cambium (*C.*). C, a tetrarch root after secondary thickening has been going on for some time. *Co.*, cork; *Cor.*, cortex; *En.*, endodermis; *Ph.*, phloem; *P.r.*, primary ray; *P.xy.*, protoxylem; *Xy.*, primary xylem; 2*Xy.*, secondary xylem.

than in the stem, so that the annual rings are usually less conspicuous. In its detailed structure the *secondary phloem* is similar to that of the stem, and, except for the points already mentioned, the same is true of the secondary wood. In the root, as in the aerial axis, the production of secondary tissues forces the primary phloem progressively farther from the centre. Old, secondarily thickened roots resemble stems very closely, but, when the central tissues are preserved, the original root-structure can be traced by following down the primary rays and locating the protoxylem-groups at the periphery of the metaxylem.

The storage of food in *fleshy roots* is effected by thin-walled

parenchyma, which is often copiously developed both in the secondary phloem and in the secondary xylem. The vessels of the latter then form isolated groups, which are either scattered or arranged in radial files (*e.g.* Salsify, *Tragopogon*, Fig. 52, A) in the storage tissues, a distribution facilitating rapid transference from the storage cells when growth is resumed. In such roots the limits of secondary xylem and phloem are often difficult to distinguish, unless the cambium be first located; moreover, the primary xylem is often indistinguishable.

The process of secondary thickening so far described is that normally found in the vast majority of Dicotyledons and Conifers, but a few so-called *anomalous types* merit a brief consideration. In many members of the Spinach-family (Chenopodiaceæ) the normal cambium functions only for a short time and, after forming a narrow strip of secondary xylem and phloem, ceases to divide. Thereupon another cambium arises in the inner part of the cortex, and a new strip of xylem and phloem is produced till this cambium in its turn ceases to be active. This process is repeated again and again, each successive cambium forming xylem on the inner and phloem on the outer side. In the root of the Beet (*Beta*) the successive cambia form continuous rings of xylem and phloem, its fleshy character being mainly due to the extensive development of the latter tissue. In most stems showing this kind of abnormal thickening, however, xylem and phloem are produced only in certain sectors, and appear as secondary bundles separated by the thick-walled ground-tissue, developed from the remaining parts of each cambium (e.g. *Obione portulacoides*).

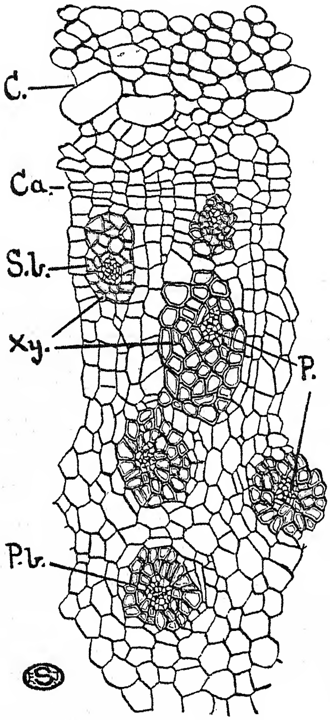


FIG. 110. Transverse section of a portion of an old stem of *Dracæna* showing secondary thickening. *C.*, cortex; *Ca.*, cambium; *P.*, phloem; *P.b.*, primary bundle; *S.b.*, secondary bundle; *Xy.*, xylem.

Another uncommon method, shown by certain Monocotyledons

which exhibit marked secondary increase in girth, is well illustrated by the Dragon-tree (*Dracæna*), the stems of which may attain a diameter of ten feet or more. The bundles of the young stem here exhibit the usual scattered arrangement; but in the cortex, immediately beyond the vascular region, there arises a cambium (Fig. 110, *Ca.*) which cuts off segments mainly towards the inside, the small number cut off on the outside forming an addition to the cortex (*C.*). Some of the inner segments divide and undergo gradual differentiation to form *secondary bundles* (*S.b.*), whilst the remainder, retaining a somewhat radial arrangement, become thickened and lignified. The secondary bundles embedded in this thick-walled tissue are concentric with centrally placed phloem (*P.*), which is often very scanty in amount; the xylem contains no vessels, consisting of fibrous tracheids only.

Very complicated types of anomalous thickening are exhibited by the woody climbers (*lianes*) of tropical forests. In many of these the old trunks develop cambial rings about several centres, each such cambium producing a separate xylem-core, so that a rope-like structure composed of several intertwined woody strands results.

CHAPTER XVII

CORK-FORMATION AND THE BARK

ONE result of secondary thickening is a marked enlargement of the periphery of stem or root, in consequence of which the outer tissues are subjected to increasing tension (cf. p. 172). These, the epidermis and cortex, ordinarily have but a limited power of stretching, and, as soon as this limit is reached, they rupture and no longer form an effective covering for the underlying tissues. This function is henceforth fulfilled by a protective tissue, the *cork*, formed by the active division of a secondary meristem, the phellogen or cork-cambium, which arises in the cortex. In a few plants (e.g. *Acer striatum*) the epidermal and cortical cells are capable of limited growth and division, and here the formation of a cork-cambium is correspondingly delayed.

Cork-formation takes place in essentially the same way in both stem and root. The *phellogen* invariably arises by the formation of two successive tangential walls, in the stem most commonly in the cells of the subepidermal layer (Fig. 111). The cells are thus each divided into three segments, of which the central constitute the actual cork-cambium (*c.c.*), whilst the outer form the first layer of cork and the inner the first, and often the only, layer of a tissue known as *phelloderm* (*Ph.*). Whilst the outer and inner segments undergo no further division, the cells of the phellogen divide again and again, one of the two products of each division becoming differentiated as cork or phelloderm, while the other remains as the cell of the cork-cambium. Usually, however, these divisions of the phellogen lead to the cutting-off of cells on the outside only, so that no further formation of phelloderm takes place.

The activity of the phellogen results in the development of a continuous cylinder of tissue consisting of numerous radial files of cells, each file (Fig. 111, 1–6) representing the product of one cork-cambium cell. This tissue is the cork and, apart from the absence of intercellular spaces between its cells, it is especially characterised by a chemical modification of the cell-walls spoken of as *suberisation*. This latter renders them practically impervious

alike to gases and to liquids, features to which cork owes its utilisation in closing bottles.

Suberisation is due to the deposition of a layer of fatty compounds on the inner surface of the wall, and hence cork is coloured by the same reagents (Scharlach red, etc.) as stain fats. A yellow-brown colouration is assumed with chlor-zinc-iodide, and a yellow one with strong potash. On boiling with concentrated potash,

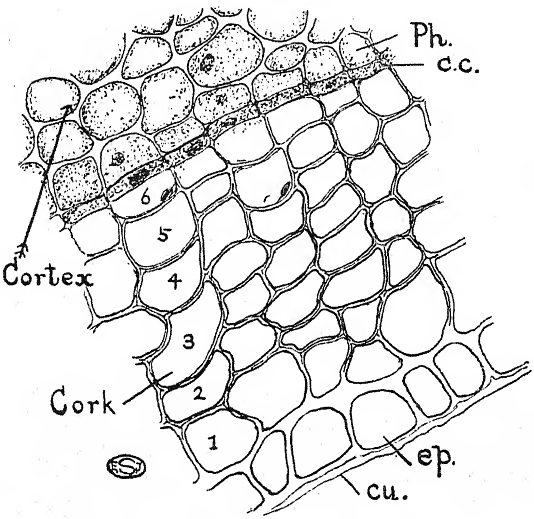


FIG. 111. Transverse section through the cork layer in the stem of the Elder (*Sambucus*). *c.c.*, cork-cambium; *cu.*, cuticle; *ep.*, epidermis; *Ph.*, phelloderm; 1–6, successive segments of the cork in order of production.

large yellow globules often escape from the walls. Suberised membranes, moreover, are highly resistant, being insoluble both in cuprammonia and concentrated sulphuric acid. Suberisation of the walls ensues soon after the cork-cells are cut off from the phellogen, and it is almost unnecessary to add that, as a result, the cells die, their contents ultimately consisting of air or more rarely of pigmented bodies (often tannins and their derivatives). The characteristic white appearance of the surface of the Birch (*Betula*) is due to the presence in the cells of the cork of solid granules of a substance known as betulin.

The cells of the *cork* vary considerably in shape, although very commonly flattened. The walls are often relatively thin. The radial walls are frequently thrown into folds, whilst the tangential ones are often almost straight (cf. Fig. 111). These features of

the cork-cells can be related to the tangential tension and radial compression set up by the increasing girth of the enclosed axis.

In a few plants (*e.g.* Currant, Fig. 112, Laburnum, etc.) a more or less extensive *phelloderm* (*Ph.*) is formed. The cells of this

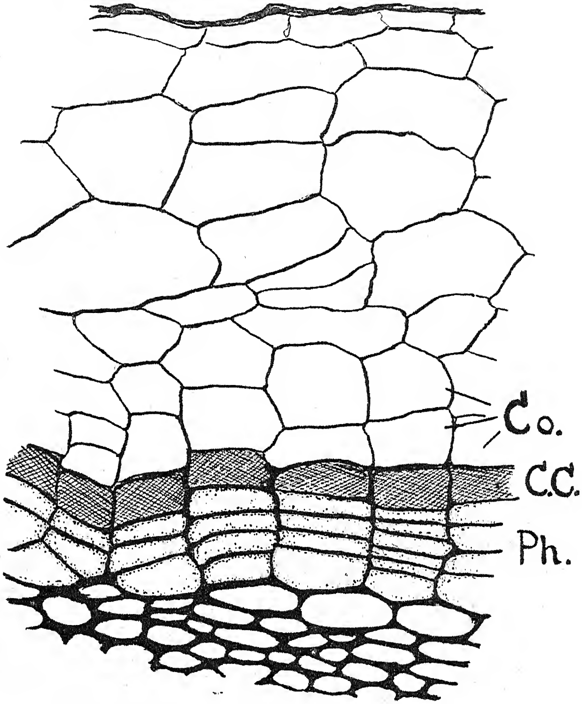


FIG. 112. Transverse section through the peripheral part of the stem of the Currant (*Ribes*), showing the cork (*Co.*), the cork-cambium (*C.C.*), and the extensive phelloderm (*Ph.*), of four to six layers of cells. Beyond the cork are seen cortex and epidermis.

tissue also are arranged in radial files, but the walls remain unsuberised. The phelloderm consists of living cells, and thus merely serves to augment the primary cortex, although where the walls are thickened it has an additional mechanical value.

Whilst the cork-cambium most commonly develops in the subepidermal layer of cells, it not infrequently arises in deeper-seated cortical layers (Fig. 112) or even in the pericycle. A good instance is furnished by the Barberry (Fig. 113), where the phellogen (*C.C.*) develops just inside the ring of mechanical tissue (*Sc.*) occupying the inner part of the cortex. In roots, too, it almost

invariably arises in cortical cells in the immediate neighbourhood of the pericycle (Fig. 109, C, *Co.*). The origin of a cork-cambium from the epidermis is seen in Willows, as well as in the Rose, Apple, Hawthorn, and other members of the Rosaceæ.

The cork not only prevents the excessive transpiration which would ensue from rupture of the epidermis consequent upon secondary thickening, but also takes over other protective functions of that tissue. Suberised walls possess considerable strength, though their elasticity is slight, and the cork consequently forms a mechanical envelope whose efficiency is heightened by the close connection between its cells. The frequent presence of air in the latter retards excessive heating by day or excessive cooling by night. Moreover, the waste substances commonly encountered in the walls or cavities of the cork-cells are antiseptic, excluding access of various parasites to the living tissues within. As soon as cork-development commences, therefore, the parts concerned become ensheathed in an almost impermeable protective layer which would practically sever all direct communication between the internal tissues and the atmosphere, but for the formation of localised patches of loose tissue, the *lenticels*, whose development often commences slightly before that of the cork.

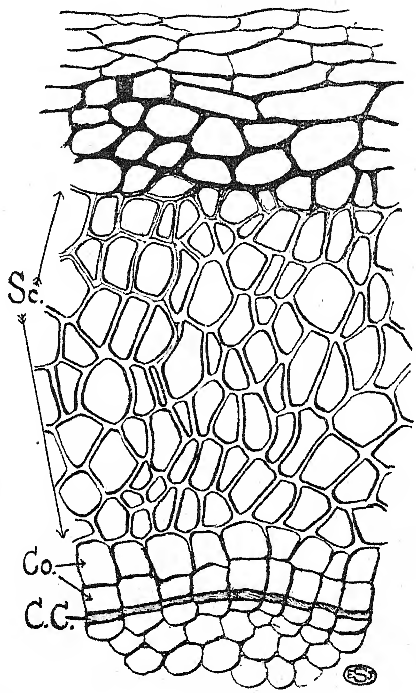


FIG. 113. Transverse section through the deep-seated cork in the stem of the Barberry (*Berberis*) showing two layers of cork-cells (*Co.*) situated between the cork-cambium (*C.C.*) and the zone of sclerenchyma (*Sc.*).

The first lenticels usually arise beneath the stomata of the young stem, where strips of cambium are formed in the subepidermal layer by the customary tangential divisions. These cambial strips divide very actively, cutting off segments on both sides. Those on the inner give rise to radial rows of phelloderm,

whilst those on the outer remain thin-walled and unsuberised, but sooner or later round off and frequently lose all connection with one another (Fig. 114, *l.*). This loose tissue [1] is formed in considerable bulk, so that it leads to a gradual elevation and ultimate rupture of the overlying epidermis. The tissue of the lenticel is thus exposed, and air from the external atmosphere can freely circulate between its cells and, by way of the narrow air-spaces between the cells of the phellogen and phelloderm, into the intercellular spaces of the cortex. The rounding-off of the constituent

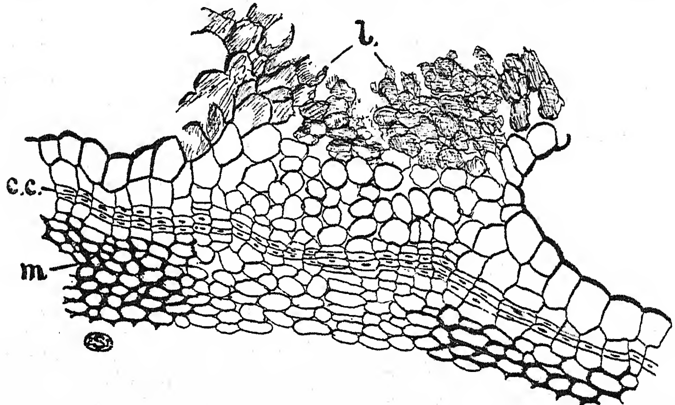


FIG. 114. Transverse section through a lenticel (*l.*) of the Elder (*Sambucus*). *c.c.*, cork-cambium; *m*, mechanical tissue.

cells and consequent development of the intercellular spaces vary considerably, so that the lenticel may be spongy (*e.g.* Elm, Birch) or relatively compact (*e.g.* Willow, Spindle-tree). In some lenticels alternating zones of loose and compact tissue are formed. The strips of cambium giving rise to the lenticels subsequently become continuous with the cork-cambium (Fig. 114).

Where the cork is deep-seated, the tissues external to it are practically cut off from all sources of food and all connection with the interior, and therefore die away. These dead tissues, on the outside of the cork, are shed sooner or later, leaving the latter exposed as *bark*. In some plants (*e.g.* Beech, Oak) the same cork-cambium continues to divide year after year, although inactive during the winter, so that a thick mass of cork is formed. This is also true of the Cork Oak (*Quercus suber*), which is the main source of the commercial article. In this tree the first cork, which here arises subepidermally, is of no value, being removed when the tree is ten to fifteen years old. The cortex thus exposed forms a

[1] Forming the so-called "complementary tissue."

new phellogen which gives rise to the thin-walled cork of commerce. This is peeled off every eight to twelve years. The corks for bottles are cut in such a way that the long dark lenticels traverse them transversely.

In most woody plants the first-formed phellogen ceases to divide, and indeed itself becomes changed into a layer of cork, at a comparatively early stage. A new cambium then arises at a deeper level in the cortex, produces a fresh zone of cork, and then in its turn passes out of action, to be succeeded by another situated still deeper. The bark formed in this way consists of alternating layers of cork and dead cortex, and comprises all the tissues beyond the most recently established phellogen. When the original cork-cambium is deep-seated, the subsequent cambia are continuous cylinders; whilst when the first is superficial, the later ones are often merely curved vertical plates whose margins are in contact with one another. As the bark gets thicker and thicker the outer portions are subjected to a growing tension, so that, being dead tissue, fissures appear at the surface as irregular longitudinal furrows well seen in the Oak and Elm. In many plants, however, the oldest bark is shed, and this takes place either as rings (*ring-bark*, *e.g.* Birch, Cherry) or as scales (*scale-bark*, *e.g.* Plane, Scot's Fir), according as the successive cork-cambia are continuous cylinders or separate plates.[1]

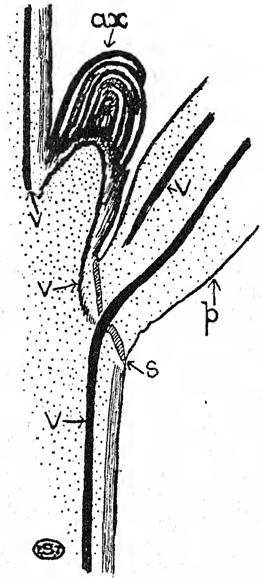


FIG. 115. Diagrammatic longitudinal section through part of a node of the Sycamore (*Acer pseudoplatanus*), showing the abscission layer (*S*.). *ax*., axillary bud; *p*., petiole; *V*., vascular bundles.

After the shedding of the first-formed cork, lenticels may develop from any part of an active phellogen. As a result of subsequent stretching they assume various forms, which are often characteristic of individual species. Thus, on the bark of the Birch and Cherry they appear as slightly raised horizontal lines, whilst in the Poplar they are usually lozenge-shaped. The *cork-wings* developed in many varieties of woody plants (*e.g.* Cork Elm, Cork Maple, etc.) are due to the copious formation of cork which, consisting as it does of dead cells, necessarily splits at the surface; the regularity of the fissures may,

[1] Regarding commercial uses of bark, see pp. 79, 89, 91.

however, depend in part on excessive local activity of the cork-cambium.

It will have become apparent that cork serves to protect surfaces which would otherwise be exposed, and indeed it is even found covering wounds and the scars left by the shedding of leaves, flowers, branches, etc. The fall of leaves is preceded by the differentiation of a definite separating layer (*abscission layer*) which is produced, with or without division, from the cells at the base of the leaf-stalk (Fig. 115, *S.*). The layer in question is generally recognisable by the smaller size of its cells, and its position is often indicated externally by a slight constriction of the petiole. Subsequently the middle lamellæ between the cells of this layer become mucilaginous and break down, so that for a short time the leaf is connected with the stem solely by the epidermis and vascular bundles. Beneath the abscission layer a protective layer of cork, which subsequently becomes continuous with that of the stem, is developed, either before or after the detachment of the leaf. The smooth layer of cork covering the leaf-scar is interrupted only where the vascular bundles are broken across, and here the vessels are usually plugged by tyloses (p. 178). The detachment of flowers and the phenomenon of self-pruning, by which small branches of certain trees (*e.g.* Poplar) are regularly shed, is due to a similar development of a definite abscission-layer.

CHAPTER XVIII

THE PLANT IN RELATION TO ITS WATER-SUPPLY [1]

IT has been emphasised that the root subserves several functions, of which the most important are anchorage and absorption. The latter takes place over the whole surface of the young root, but especially by means of the root-hairs in virtue of the suction-force (p. 45) established in the living cells. Since transpiration is under most conditions taking place from all the exposed surfaces of the shoot, a suction-gradient is maintained throughout the plant so that water passes from the absorbing surface of the root towards the leaves. The water around the contiguous soil-particles is thus continually being drawn into the root-hairs and, in its place, further moisture flows in from the surrounding soil; the cell-sap of the root-hairs thus becomes diluted (*i.e.* weaker than that of the cells of the cortex), so that water will begin to flow inwards (see the arrows in Fig. 116). In this way it gradually moves towards the centre of the root, even across turgid cells, and thus ultimately reaches the vessels, whence it passes to the stem and leaves. The rate of absorption of water is greatly affected by the temperature of the soil, but the range of temperature, which is of chief importance, varies with the kind of plant concerned.

Since the vessels commonly contain a solution of lower osmotic concentration than the living cells of the cortex, water evidently passes into the vessels against the osmotic gradient. It is not altogether easy to account for this in the present state of our knowledge, but since experiments have shown that absorption of water and mineral salts is dependent upon active respiration of the roots, the latter process would appear to provide the energy necessary for such transference across an osmotic gradient.

[1] Important books on general physiology of plants are: W. Stiles, *An Introduction to the Principles of Plant Physiology*, Methuen, 1937 (615 pp.); and E. C. Miller, *Plant Physiology*, McGraw Hill Book Co., 1931 (900 pp.). The water-relations of plants are considered in detail in N. A. Maximow, *The Plant in Relation to Water* (transl. by R. H. Yapp). Allen & Unwin, 1929 (451 pp.).

At certain times the water indeed appears to be pumped into the wood with great vigour, so that a considerable upward pressure (so-called *root-pressure*) is manifest. This may be demonstrated in the following way: The stem of a plant of the Fuchsia or Vegetable Marrow growing in a pot is cut off about 2 inches above the level of the soil. To the cut stump one of the horizontal arms of a T-tube is firmly connected by a short length of pressure tubing, both joints being wired on. To the other horizontal arm is attached about 3 inches of similar tubing, the free end of which

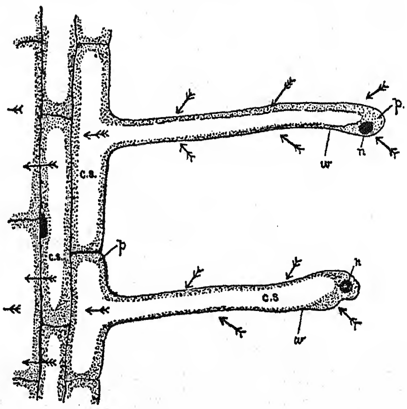


FIG. 116. Diagram of surface-cells of root with two root-hairs (very considerably magnified). The direction taken by the water is indicated by arrows. *c.s.*, cell-sap; *n*, nucleus; *p*, cytoplasm; *w*, cell-wall.

can be closed by a clip. After filling the T-piece with water, a mercury manometer is joined on to the vertical arm, taking care to exclude all air-bubbles. The clip is then closed. The soil is well watered and the apparatus is kept in a warm place. Very soon the mercury in the manometer will register an increasing pressure and, in a sturdy plant, this may reach nearly an atmosphere.

It will be obvious that, when such root-pressure exists, it must help in forcing water up the stem, particularly when the latter is of no considerable height; an effective root-pressure is, however, in nature realised only at certain times. Such pressure also finds expression in another way, viz. in the phenomenon of *bleeding*, in which the exuded liquid collects on the cut end of the stem, as is well seen in the Cress, the Vine, and in trees felled in spring. The exuded sap is often rich in sugars (p. 177), and also contains mineral salts, which would appear to indicate an active secretion by the living cells into the dead vessels.

On damp warm nights, when there is abundant absorption and

transpiration is at a minimum, a considerable positive pressure results. The excess of moisture, in many plants, then escapes through special organs called *hydathodes*, over which it frequently collects as small drops of liquid. The hydathodes are usually situated on the margins of the leaves, *e.g.* at the ends of the principal veins of the peltate blade of the Garden Nasturtium (Fig. 117, B), at the tip of the leaf in Grasses (Fig. 117, A), or upon the leaf-teeth in the Marsh Marigold and Fuchsia. If any one of these

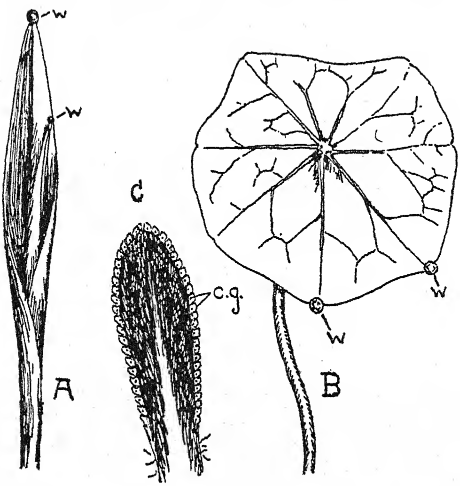


FIG. 117. Leaves with water-pores. A, Maize. B, *Tropæolum* (peltate leaf). C, Saxifrage with chalk-glands (*c.g.*). *w*, the drops of water above the water-pores.

plants, in a well-watered condition, is placed beneath a bell-jar in a warm moist atmosphere, the drops of liquid marking the positions of the hydathodes soon appear. They can be demonstrated more rapidly by the application of a negative pressure in the surrounding atmosphere (cf. p. 200, Fig. 122, C).

In some plants the hydathodes take the form of glandular hairs, their cells possessing dense protoplasmic contents and large nuclei. Good examples are found on the leaves of the Runner Bean (Fig. 118, A), where they are bent, club-shaped structures situated near the veins and consisting of a row of thin-walled cells, the terminal cell often being divided into two by a vertical wall.

A hydathode, exhibiting quite a different mechanism, is much commoner among British plants. These hydathodes occur generally above the bundle-endings, being especially located at the leaf-apex (Grasses) or on the tips of the leaf-teeth (Lesser Celandine). In these the water escapes from so-called *water-pores*, which

are situated in the epidermis of the hydathode (Fig. 120, *St.*) and

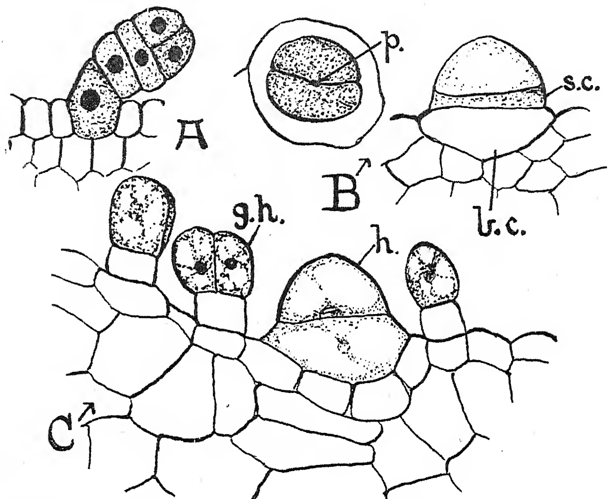


FIG. 118. Water-secreting hairs. A, Runner Bean (*Phaseolus multiflorus*). B, Yellow Rattle (*Rhinanthus*). C, Toothwort (*Lathræa squamaria*). The left-hand figure of B from the surface, the others in vertical section. *b.c.*, basal cell; *g.h.*, glandular hair; *h.*, hydathode; *p.*, pore; *s.c.*, stalk cell.

resemble ordinary stomata, except that they are often larger and that their pore remains permanently open in correspondence with the absence of the characteristic thickenings in the guard-cells; in surface sections they chiefly differ in their more rounded form (Fig. 119). In some plants but a single water-pore is associated with each hydathode (*e.g.* Enchanter's Nightshade, *Fuchsia*), but in others they are numerous (*e.g.* Wild Strawberry), and occasionally grouped in shallow depressions that can be recognised with the unaided eye (*e.g.* Marsh Marigold).

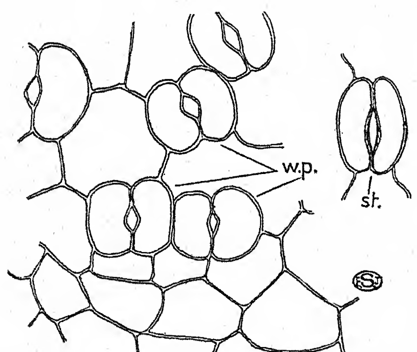


FIG. 119. Water-pores (*w.p.*) of the Lesser Celandine (*Ficaria verna*) seen from the surface; *st.*, a normal stoma on the same scale for comparison.

In a longitudinal section through an entire hydathode of this type (Fig. 120) the end of the vascular bundle, which is here seen

to consist of tracheids only, usually enlarges somewhat, often in a cup-shaped manner. Between the tracheids and the overlying water-pores there is commonly a small-celled tissue, the *epithem* (*ep.*), composed of cells with prominent nuclei and dense cytoplasmic contents; there is often, however, a space immediately beneath the epidermis. The epithem is traversed by a system of fine intercellular spaces through which, under sufficient pressure, the water passes from the tracheids to the water-pores.

Hydathodes can often be recognised at a very early stage, and are probably most active in the young leaf, which develops in an almost saturated atmosphere within the expanding bud. Active

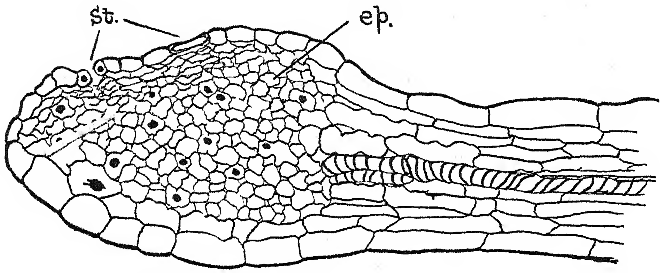


FIG. 120. Hydathode of Lesser Celandine (*Ficaria verna*) in vertical section (after Salisbury). *ep.*, epithem tissue; *St.*, water-pores.

exudation of water takes place when the hydrostatic pressure within the plant becomes excessive. The hydathodes can therefore be regarded as safety-valves which avert damage to the immature cells. The liquid exuded from hydathodes is not pure water, but usually contains a very small percentage of dissolved salts. In some plants, however, the amount of the latter may be so considerable that they remain behind as an incrustation when the water evaporates. Thus in the Saxifrages (*Saxifraga*) and the Sea-Lavender (*Statice*) a little white scale consisting of carbonate of lime is often found in dry weather on the leaf-teeth over each of the hydathodes.

The exudation of water from hair-like hydathodes is due to active secretion on the part of the protoplasts of the constituent cells. As a consequence secretion of water ceases, if the cells be killed by painting the surface of the leaf with a solution of corrosive sublimate or other poison. Hydathodes possessing water-pores are, however, mainly passive in their action, the water being forced out by hydrostatic pressure through the intercellular spaces of the epithem, and not by active secretion on the part of the living protoplasm.

Nectaries of flowers (cf. p. 451) represent a form of secretory organ comparable to the hydathodes just considered. The nectar is produced by the active secretion of cells belonging either to the modified epidermis (usually palisade- or papilla-like, e.g. *Anemone nemorosa*) or to the underlying tissue. The nectary of the Hogweed or other common member of Umbelliferæ, forming the disc on the top of the ovary, is seen in a cross-section to consist of a mass of small glandular cells having the customary thin walls, abundant protoplasm, and large nuclei, and covered by an epidermis containing numerous stomata. The prominent cuticular ridges often exhibited by the epidermis of these nectaries may serve to retain the secreted fluid *in situ*. In the Buttercup the secreting tissue at the base of the petal is similarly composed of small cells, but there are no stomata, so that the nectar only escapes by filtration through the outer membrane.

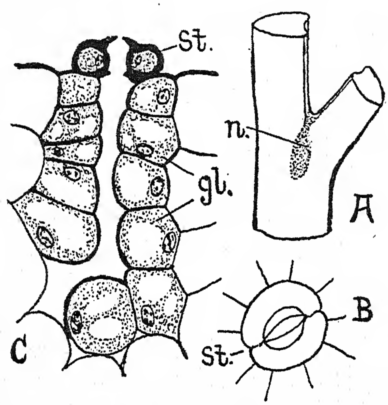


FIG. 121. Extrafloral nectary of the Bracken (*Pteridium aquilinum*) (after Lloyd). A, The fork of a frond showing the nectary (*n.*). B, A stoma from the nectary in surface view. C, The nectary in section. *gl.*, glandular cells; *St.*, stoma.

Nectaries always produce a sweet sugary fluid which at first is very concentrated (being thick and syrupy), but subsequently becomes more and more diluted by absorption of liquid from beneath. We can imitate this mechanism in a simple way by scooping out two hollows in an unpeeled Potato and filling one of them with powdered sugar. After about an hour the latter cavity will be found full of syrup which may even overflow, whilst the other is dry and empty. In this way nectaries may serve to withdraw excess of water from the plant.

Extrafloral nectaries on the vegetative organs occur in quite a number of plants, *e.g.* on the under-surfaces of the stipules of the Broad Bean (*Vicia faba*), on the leaf-bases of the Black Bindweed (*Polygonum convolvulus*), at the forks of the fronds of the Bracken (*Pteridium aquilinum*, Fig. 121, A), and on the upper part of the petioles of the Cherry and Guelder Rose (*Viburnum opulus*, Fig. 315, F, p. 452). In the first-named plant the nectary appears as a dark depression, which when cut across is found to be composed of a palisade-like layer of secreting hairs, each consisting of an

oblong head of several cells, borne on a short stalk. In the Guelder Rose the nectaries take the form of short cup-like projections, each supplied with a vascular bundle, the actual secreting surface being situated in the depression at the tip, and being similar in structure to that of the floral nectary of the Hogweed. The structure of the nectaries of the Bracken will be apparent from a reference to Fig. 121, C.

The osmotic substances secreted by extrafloral nectaries tend to withdraw water from the plant when it is turgid, and these organs are indeed most active in a moist warm atmosphere. They may well serve primarily, therefore, to fulfil the same purpose as hydathodes. Floral nectaries, however, have in addition the important function of attracting insects.

The xylem has been recognised as the channel through which the water passes. Further evidence is supplied by the fact that a ringed branch (*i.e.* one from which all the tissues outside the wood have been removed for a short distance) remains healthy for weeks if left on the plant or kept in water under suitable conditions. The moisture can, therefore, be travelling only through the wood or the central pith, but since the latter completely disappears from the mature stem of many plants (p. 138), it is obviously not essential for water-conduction.

The rate of flow of the water through the wood varies greatly from plant to plant and, for instance, with the same driving force is appreciably less through a Coniferous than through most Dicotyledonous stems, a fact which can be shown in the following way (Fig. 122, A): A round-bottomed flask is provided with a two-holed rubber cork, through each hole of which a piece of glass tubing twice bent at right angles is inserted (as in the figure). The one arm of each glass tube should project only for a short distance below the cork, while the other free arm should be considerably longer. To the open end of the latter a short piece of stem (in the one case of a Conifer (*g*), in the other of an Elm (*d*), both being of equal length) is fitted by rubber tubing, so as to make an air-tight connection. Each piece of stem should be previously coated, all except its two ends, with a layer of melted paraffin-wax, so as to close up all apertures and scars. The rubber cork with attached tubing is now taken out of the flask and the latter is half filled with water which is heated until it has boiled for a minute or two. Whilst vapour still fills the flask, the rubber stopper is fitted into it, after which the flask is placed in a vessel of cold water, the unattached ends of the two stems being allowed to dip into beakers of water (Fig. 122, A). The reduced pressure within the flask, resulting from the condensation of the contained aqueous vapour, leads to a strong suction, and as a result columns of water which have traversed the two stems will form in the tubes above their upper ends, the height of each being proportional to the rate of flow (Fig. 122, A).

Through the vessels the water ultimately flows into the leaves and from these a great part is given off in the process of *transpiration*. The cobalt-method, described on p. 7, can be made a more exact

estimate of the rate of transpiration from a leaf by the use of standard colour strips [1] representing the initial (dry) and final (moist) conditions.

That transpiration is much more rapid from the lower surface of many leaves (*e.g.* Lilac) than from the upper can be shown by this method, as well as in the following way: Choosing two healthy leaves, the ends of the petioles, and in one the lower surface of the

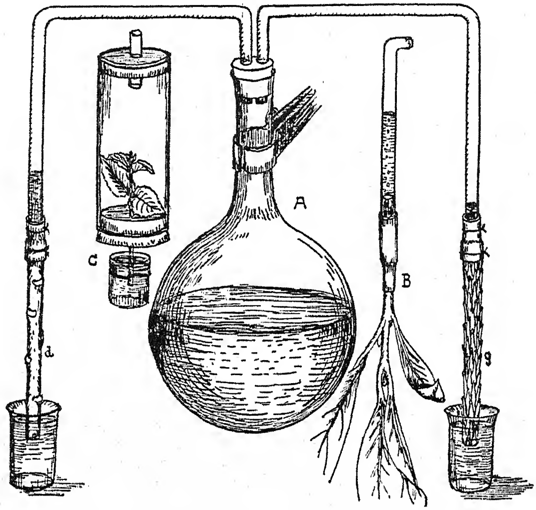


FIG. 122. A, Apparatus for comparing the rate of flow of water through the wood of two shoots (*d*, Elm; *g*, Conifer). B, Modification of same apparatus to show that there are stomata in the leaf through which gases can pass in and out. C, Modification to be used for the demonstration of water-pores. For details, see text, pp. 199, 237.

blade, in the other the upper surface, are covered with vaseline, after which the two are hung up in a warm room. A few hours later the blade vaselined on the upper side will be more or less withered, whilst the other will have remained almost fresh. Comparison in a similar manner of a thin and a leathery leaf will demonstrate the importance of a thick cuticle.

A measure of the rate of absorption of a cut shoot can be obtained with the help of an instrument known as a *potometer*. As absorption under normal conditions is closely parallel to the rate of transpiration, it can be regarded as an indirect measure of the latter. The shoots employed in experiments with this potometer should be removed from the plant some hours previously and kept in water; before use

[1] For details as to their preparation, see Henderson, *Annals of Botany*, l, 1936, pp. 321–324.

the lower 3 inches of the stem should be cut off. The potometer (Fig. 123) consists in general of a three-way glass tube; to one arm the plant is attached, to the second a funnel serving as a reservoir and capable of being closed by a stopcock, while the third arm is connected to a piece of capillary glass tubing bent downwards at the end and resting on a graduated scale. To prepare the instrument for use the stopcock is opened and water is poured into the funnel until it fills the apparatus and flows from the end of the capillary tube, whereupon the stopcock is closed.

A perforated rubber stopper is carefully passed over the end of

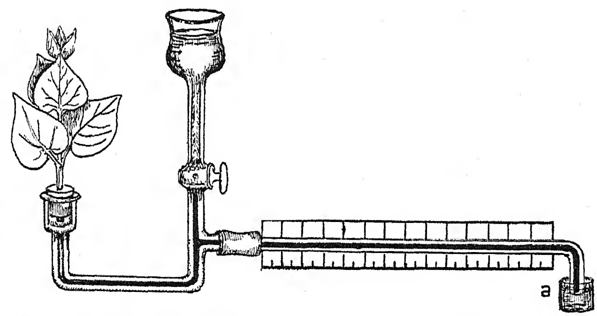


FIG. 123. Potometer. For description, see text.

a leafy shoot (see Appendix XIV) and fitted into the arm designed to take the plant so that the end of the stem is in water. The open end of the capillary tube dips into a reservoir *a*. If this be removed for a short interval, a small air-bubble is introduced which will be seen to creep along it; this is due to the fact that the moisture lost in transpiration from the leaves is replaced by absorption. By opening the stopcock, until the column of air has been driven back, and again closing it, the potometer is prepared for a fresh observation; and, if we record (with the help of a stop-watch) the time taken for the end of the air-column to pass over a measured distance on the scale, the average of several readings will give an estimate of the rate of absorption from the shoot employed.

In this way we can indirectly determine and compare the rates of transpiration from shoots of different plants, the contrast afforded by evergreen and deciduous types being specially instructive. If half the leaves of a shoot are removed or vaselined, it will be found that, as a result of the reduced transpiring surface, the rate of absorption is much decreased. We may also compare shoots exposed to different conditions, such as a hot and a cold room, dry and moist air, moving and still air, and in each instance we shall find

that the first of the two alternatives induces more active absorption. We may therefore assume that transpiration is accelerated by heat, dryness of the air and wind.

The actual amount of transpiration in a given time can be measured by placing a plant (soil and pot being covered with waterproof material) on one scale-pan of a coarse balance and putting sufficient weights on the other to counterbalance it. After some time the scale-pan bearing the plant will be found to have risen, and by adding weights to it the amount lost in transpiration can be gauged. If a perfectly accurate result were possible by this method, it would be necessary to allow for the gain in weight as a result of photosynthesis and the loss due to respiration (cf. p. 240).

Another method is to place the plant (soil and pot again being covered), together with a weighed amount of dry calcium chloride, underneath a bell-jar, whose lower edge is greased so as to make an airtight joint with a glass plate on which it rests. A control should be fitted up with an equal amount of calcium chloride, but with a covered pot having no plant. If after some time the two lots of chloride be reweighed, that from the bell-jar containing the plant will be found to be much heavier, and the difference between their weights will give the amount of water-vapour transpired. Since in this experiment the plant is transpiring into a dry atmosphere, the results are actually a measure of the resistance of the plant to desiccation.

In transpiration molecules of water are given off from the exposed surfaces of the cells adjoining the intercellular spaces in the interior of the leaf. The molecules passing through the cytoplasm and the permeable cell-walls are ultimately derived from the cell-sap. Their loss, therefore, tends to be resisted by the osmotic attraction of the contents of the transpiring cells. Hence a turgid cell gives up water much more readily than one which is flaccid, and thus the water-content of a shoot is an important internal controlling factor in the rate of water-loss. Moreover, the expansion due to turgidity presents a larger surface to the intercellular spaces. Externally the most important controlling factor is the degree of saturation of the air or the water-deficit which is mainly influenced by temperature and wind. It should be emphasised that water-loss can take place, even into a saturated atmosphere, if the temperature of the interior of the leaf be above that of its surroundings. Hence a hairy covering may reduce transpiration by checking the rise of temperature of the leaf-cells through radiation.

Owing to the importance of the degree of saturation of the air, it follows that the water-vapour given off from one stoma, by

increasing the humidity of the air around, may interfere with the diffusion of water-vapour from the neighbouring stomata. Thus, the closer together the stomatal pores, that is to say, the greater their frequency per unit area, the greater will be the mutual interference, especially in still air. There must therefore be an optimum frequency of stomata which gives the maximum number of apertures for escape of vapour with the minimum of interference. The ordinary perforated epidermis has the stomata situated at approximately this optimum distance and, as a consequence, diffusion through it, when the stomata are wide open, may take place just as rapidly as though the intercellular spaces of the leaf were freely exposed.

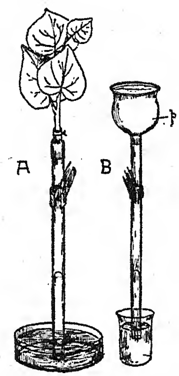


FIG. 124. A, Demonstration of suction due to transpiration. B, Demonstration of suction due to evaporation from a porous mass (p). For details, see text.

The giving off of moisture from the surface of the plant in transpiration produces a marked suction or *negative pressure,* which can be readily demonstrated by the experiment shown in Fig. 124, A. The end of a leafy shoot, cut under water and with the surface of the stem vaselined, is firmly fixed by pressure tubing into the upper end of a long narrow glass tube filled with water (see Appendix XIII), the lower end of the tube dipping into a vessel containing mercury. By slow degrees the mercury rises in the tube, replacing the water sucked up by the shoot as a result of its transpiration. That this is a purely physical phenomenon can be shown by substituting some porous mass for the shoot. The bulb of a thistle is *loosely* packed with wet Plaster of Paris (*p* in Fig. 124, B), which in setting will expand sufficiently to fill it completely. The stem of the thistle funnel is then filled with water and its lower end placed as before in mercury, when a similar gradual rise of the latter is observed. Experiments of this kind, carefully performed, have shown that the mercury will ascend to a considerably higher level than that supported by ordinary atmospheric pressure.

It will be obvious that this suction must materially assist in the upward passage of water through the plant, but the entire mechanism of the ascent of sap is far from being properly understood and involves such complicated principles that its consideration would be out of place in a book of this scope. When a plant is obtaining abundant moisture, so that absorption is in excess of transpiration (and it is at such times that root-pressure is generally

to be observed), the water in the vessels is forced upwards under a positive pressure. As soon, however, as transpiration is only just balanced by absorption, the water in the vessels is being pulled up by suction, so that it is in a state of tension. At such times some vessel-segments may be occupied not by liquid, but by water-vapour and rarefied air. That the pressure of the water in the vessels is less than that of the atmosphere, *i.e.* is under *negative pressure*, can be demonstrated as follows:

When the stem of a plant, which has recently been little watered, is cut open under a solution of light green, the dye will be found to have penetrated into the vessels to a much greater distance than in a plant which has been well watered.

It is a familiar fact that if plants are gathered on a hot summer's day, when a negative pressure is almost invariably realised, they often wither even though placed in water soon after. This is due to air being sucked up into the vessels which consequently lose their power of conducting moisture. If two shoots are cut, one under water and the other in the air, from a plant in which negative pressure has been demonstrated, the two being afterwards placed in water, the former will remain fresh, whilst the latter may soon fade. Hence the necessity of cutting shoots under water, if they are subsequently to be used for transpiration-experiments (cf. p. 200).

Plants absorb a far larger amount of moisture than they directly need, since most of it is given off again in transpiration. This process has a very slight effect in lowering the temperature of the leaves. The stream of water serves to carry the mineral salts absorbed from the soil, but there is no direct relation between the quantity of water transported through the plant and the amount of mineral salts absorbed. Excessive transpiration is a danger with which a plant has to cope, since for photosynthesis a large evaporating surface provided with pores must be exposed to the air, and this renders a heavy loss of moisture inevitable.

CHAPTER XIX

PHYSIOLOGY OF NUTRITION

THE various mineral salts in solution (cf. p. 7) in the water help in one way or another to build up the body of the plant. The water retained is employed for diverse purposes, viz. (i) in combination with the carbon dioxide of the air to form the starting-point of the organic substance of the plant, (ii) to keep the cells in a turgid condition (cf. pp. 44 and 143), (iii) to serve as a medium for transference of soluble materials from one part to another, and (iv) as imbibition water permeating the cell-walls and protoplasm. Uncombined water thus constitutes a great part of the plant, as can be readily seen by comparing the weight of a fresh and a dried plant.

To ensure a more accurate comparison a considerable quantity (*e.g.* about 100 grams) of fresh material is cut up into small pieces, put into an evaporating dish of known weight, and the two weighed together. The dish is now placed over a water-bath and heated until the weight is constant. The final weight of the material is far less than the original one. Since the temperature of the water-bath would be only sufficient to drive off the uncombined water, the loss of weight recorded corresponds to the amount of the latter; the weight of the remaining substance is consequently known as the *dry weight* and is usually expressed in percentages of the fresh weight.

The dry weight varies considerably according to the kind of plant or the portion of it used; thus, in a woody plant it amounts to about 50 per cent., in an herbaceous plant to about 30 per cent., and in a water-plant (as well as in many edible fruits) to little more than 5 per cent. In all but woody plants, therefore, the major part of the plant's substance consists of water. This does not, however, apply to dormant seeds in which the dry weight usually represents about seven-eighths of the total, and we can consequently understand why, as a preliminary to germination, so large an amount of moisture has to be absorbed (cf. p. 21).

In order to study further the composition of the plant we

place the dried material in a weighed crucible and heat it strongly for several hours over a Bunsen burner, but the temperature should not be so high as to cause it to glow. The mass first becomes charred and then gradually assumes a greyish-white colour like that of tobacco-ash. During this heating process all the carbon, hydrogen, oxygen, and nitrogen compounds composing the plant are broken down and escape, chiefly in the form of various simple gases (*e.g.* carbon dioxide, water-vapour, free nitrogen, etc.), and the matter that remains (the so-called *ash*) consists of the mineral constituents of the plant (*e.g.* silica, potassium carbonate, etc.).

If, after cooling, the weight of the ash is ascertained, it will be found to represent but a small fraction of the original dry weight (*e.g.* about 4 per cent. in a Potato, about 7 per cent. in the Clover, and as much as 17 per cent. in Tobacco-leaves). In order to obtain a fairly accurate estimate of the ash the heating must be repeated until no further decrease takes place. Analysis of the ash (Appendix VIII) of a large number of plants has shown that it always contains compounds of the following elements, though present in varying amounts: aluminium, calcium, chlorine, iron, magnesium, phosphorus, potassium, silicon, sodium, sulphur. To these must be added the elements carbon, hydrogen, nitrogen and oxygen, which were present in the dried material before its conversion into ash, so that compounds of a considerable number of chemical elements are always to be found in the plant. That some of these are really essential can be shown by growing plants in so-called *water-cultures*.

For the setting up of water-cultures (Fig. 125, see also Appendix IX) we require a number of large jars, the interiors of which are sterilised by first rinsing them out thoroughly with commercial nitric acid and then washing out the latter with boiled water, until it gives no indication of an acid reaction with litmus. The sides of the jars are then covered with black paper to exclude light, and each is fitted with a cork pierced by three holes; through two of these a short length of glass tubing is inserted, whilst the middle one is left open to receive the plant. One jar is now filled about four-fifths full of glass distilled water, whilst a second receives a culture-solution made up as follows:—

Potassium nitrate	2 grams.
Magnesium sulphate	½ gram.
Calcium sulphate	½ gram.
Ferric phosphate	½ gram.

These salts are added to two litres of glass-distilled water, the whole being shaken up or thoroughly stirred, until the bulk of the ingredients have passed into solution. A small quantity of undissolved matter may remain, but this is later dissolved by the roots of the plants.

A young seedling (preferably, if a rapid result be desired, of some plant with scanty food-reserves in its seeds) is now inserted through the middle hole

of the cork in each jar, so that its roots just dip into the water, the plant being kept in position by packing it round with cotton-wool. The glass tubes, whose upper ends are closed with plugs of cotton-wool, serve for the daily aeration of the liquid in the jar and also for the addition of fresh distilled water, when necessary.

After some weeks plants growing in distilled water have a starved and stunted appearance, whilst those in a full culture-solution flourish; this shows that the compounds in the latter are sufficient for its growth, whereas water alone is inadequate.[1] If now culture-solutions are prepared, each lacking *one* of the elements in the above formula (Appendix IX), it can be proved that each is necessary for healthy growth. Thus, if nitrogen be absent (which can be effected by substituting potassium sulphate for potassium nitrate in the culture-solution given on the previous page), the seedlings fail to reach any considerable size and sooner or later die. This shows that the great volume of free nitrogen in the atmosphere cannot be used directly by the ordinary plant.

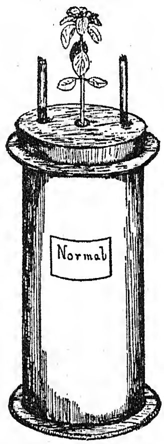


FIG. 125. Water-culture.

In the absence of a suitable supply of nitrogen no proteins or protoplasm can be formed and growth is impossible after the food reserves in the seed are exhausted; for a similar reason, if sulphur or phosphorus be lacking, no appreciable growth can take place. The element calcium is not only important in forming the calcium pectate of the cell-wall, but like potassium also plays a part in the building up of protoplasm, although both elements need not necessarily enter into its final composition. Magnesium is an actual constituent of chlorophyll, and also enters into the composition of some proteins, whilst iron appears to be mainly important in the process of formation of the green pigments. When compounds of these elements are altogether absent (which is difficult to secure owing to the presence of iron as an impurity in most chemicals), the leaves become cream-coloured or *chlorotic*. In nature, in the presence of a high calcium-content in the soil, magnesium and iron may be deficient in the plant owing to difficulties of absorption and thus chlorotic effects may result.

Experiments with water-cultures show that the following nine

[1] Both plants can of course obtain carbon in the ordinary way from the carbon dioxide of the atmosphere.

elements are essential for the nourishment of the plant: calcium, hydrogen, iron, magnesium, nitrogen, oxygen, phosphorus, potassium, and sulphur; to these we must add carbon (cf. p. 9). All of these, with the exception of carbon, are obtained from the soil in the form of simple soluble inorganic compounds like those used to make up the culture-solution. Minute traces of other elements (boron, manganese, etc.) may be highly beneficial or even essential to the proper nutrition of higher plants.

Some of the minerals in the soil are only slightly soluble in water, but the carbon dioxide given off from the surface of the root-hairs in respiration (p. 9) unites with the soil-water to form carbonic acid; this has considerable solvent powers, and thus the plant itself brings into solution some of the compounds which it requires. The corrosive action of root-hairs is shown by planting seeds in soil just above a piece of polished marble (or the inner face of a mussel-shell), when after about a fortnight the surface is found to be etched, where it was in contact with the roots.

A striking feature of the absorptive process is that different kinds of plants growing side by side in the same soil take up some compounds in very diverse amounts. Thus, the ash of Grasses consists largely of silica, to which the hard surface is due, whilst that of other meadow-plants contains but little. Similarly Seaweeds contain as much as 0·5 per cent. of iodine in their ash, so that until relatively recent times it formed the principal source of this element, although iodides are only present in sea-water in exceedingly minute quantities. It may again be emphasised that continued absorption of a mineral substance from the soil is mainly dependent on its utilisation and modification within the plant, so that the diffusion-gradient is maintained (p. 48). Absorption of mineral salts apparently only goes on while the root is actively respiring.

Turning to the process of photosynthesis it may first be noted that it is impossible to replace the carbon dioxide of the atmosphere by carbon-compounds in the soil. This can be shown by growing a plant in a normal culture-solution in an atmosphere lacking carbon dioxide and noting the subsequent absence of starch in the leaves as compared with a control. The removal of carbon-dioxide can be effected by growing the plant under a bell-jar provided at the top with an aperture which is fitted with a U-tube filled with soda lime; the latter substance is also placed around the pot or culture vessel. In the control pieces of chalk are substituted for the soda lime.

The carbon dioxide, which is thus indispensable in the formation of carbohydrates in green leaves, is found only in small amount in

the atmosphere (about three parts in 10,000 of air) and obtains access through the stomata (p. 152). For, if the under sides of the leaves of a Lilac-shoot be covered with vaseline, the shoot having previously been kept in the dark until all the starch has disappeared, none will be formed on exposure to light. On the other hand, a control shoot gives the starch-reaction (p. 8) after a short time. The continued diffusion of carbon dioxide through the stomata is dependent on a diffusion-gradient being maintained by the utilisation of the gas in the palisade and other photosynthetic cells. Hence, when the stomata are wide open, the ordinary epidermis is just as efficient as it is in the escape of water-vapour (cf. p. 203).

The importance of *chlorophyll* in photosynthesis was illustrated by the experiment described on p. 8; its importance can also be shown by applying the iodine-test to variegated leaves (*e.g.* variegated Privet, cf. p. 166).

Chlorophyll is now known to consist of two green pigments (chlorophyll *a* and chlorophyll *b*) and two yellow pigments (carotin and xanthophyll), the former being present in considerably greater quantity than the latter. The chlorophylls, which differ but slightly from each other, are complex compounds of carbon, hydrogen, oxygen, nitrogen, and magnesium, the last forming the central atom of the molecule. The yellow pigments are of simpler composition; carotin has the formula $C_{40}H_{56}$, and xanthophyll the formula $C_{40}H_{56}O_2$. A rough separation of the green and yellow pigments may be effected by shaking up an alcoholic extract with benzene and allowing the liquids to settle; the alcohol then contains the yellow, the benzene floating above it the green, pigments.

A chlorophyll-solution (see p. 8) has a deep green colour when held up to the light, but when held against a black background, so that the light is reflected from it, the solution appears a dark reddish-green (red fluorescence). If daylight, or other white light, that has passed through a chlorophyll-solution be examined with a spectroscope, a dark absorption-zone will be readily recognised in the red part of the spectrum; other absorption-zones (in the orange and yellow regions) are also present, but these are smaller and more difficult to see, whilst a large part of the blue and violet region is obliterated (Fig. 126).

It has already been mentioned (p. 207) that in the absence of iron and magnesium chlorophyll is not formed, and a similar result is seen in plants grown in the dark[1] (p. 8). Apart from these essentials for chlorophyll-formation, a suitable temperature is also necessary, the pale colour of the shoots of many plants that

[1] Such an absence of chlorophyll through growth in the dark is exhibited by the leaf-stalks of cultivated Celery and Sea Kale.

commence to grow early in spring being a result of imperfect production of the green pigments. We may recall that intense light is injurious to chlorophyll. If two test-tubes containing a solution of it are kept, the one in strong light, the other in darkness, the former will soon lose its fresh green colour (in contrast to the

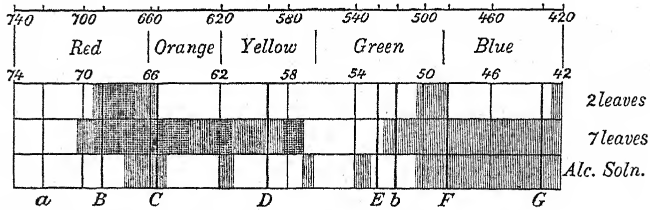


FIG. 126. Spectrum of chlorophyll (after Reinke, from Pfeffer). The lowest sector shows the absorption by a chlorophyll-solution, and the two upper sectors the light absorption by two and seven leaves respectively.

latter) and become a dirty brown, unless access of air is rigorously excluded.

The light absorbed by chlorophyll from the different regions of the spectrum is mainly important in furnishing the energy necessary for the manufacture of sugars, although its rôle is evidently very complex. The necessity of light for starch-formation (see p. 8) can be shown, if half the leaf of a plant, which has been kept in darkness till it shows no starch-reaction, is covered over with silver paper, whilst the other half is left exposed, when starch will be formed only in the illuminated part. Or, if a similar leaf is covered with a stencil-plate (Appendix XVI) and placed in the light, subsequent treatment with iodine will give a dark letter on a light ground (cf. Fig. 127). In interpreting such experiments, however, it must be borne in mind that photosynthesis may be carried on without the sugars being converted into starch. Thus, while starch-formation is evidence of photosynthesis having taken place, its absence does not necessarily prove the contrary.

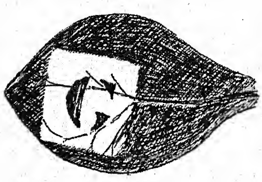


FIG. 127. Starch-print. The leaf has been covered with a stencil-plate, exposed to sunlight, decolourised and placed in iodine solution.

It is known that starch is not really the first substance formed in photosynthesis,[1] but that hexose sugars (*e.g.* grape sugar, $C_6H_{12}O_6$)

[1] For further information on photosynthesis, see the books on the general physiology of plants cited on p. 193; also W. Stiles, *Photosynthesis*, Longmans, Green & Co., 1925 (268 pp.); and B. M. Duggar *et al.*, *Biological Effects of Radiation*, 2 vols., McGraw Hill Book Co., 1936.

probably intervene; in fact, in many Monocotyledonous plants the leaves rarely produce starch (except in the guard-cells of the stomata), sugars being the customary final product of photosynthesis. But in most Dicotyledons these sugars undergo the further change into starch, and it is not difficult to show that such a conversion can take place. If detached starch-free leaves of the Canadian Pondweed are placed in a 5 per cent. solution of grape sugar in the dark, starch can subsequently be demonstrated in them.

The complex chemical changes involved in the production of carbohydrates like grape sugar from carbon dioxide and water can be illustrated by the following equation:—

$$\underset{\text{Carbon dioxide.}}{6CO_2} + \underset{\text{Water.}}{6H_2O} + 674 \text{ calories} = \underset{\text{Grape sugar.}}{C_6H_{12}O_6} + \underset{\text{Oxygen.}}{6O_2}.$$

Chemists have not yet succeeded in carrying out this process. There is no doubt that such a relatively complicated body as grape sugar is not the first to be formed, but it has not yet proved possible to ascertain certainly what substances precede it. It is held by some that formaldehyde (CH_2O) is the first product of photosynthesis. At all events it appears certain that the process involves a whole series of reactions, only some of which depend on the supply of energy in the form of light, whilst the sequence also involves enzyme-reactions.

When a relatively complicated substance like a carbohydrate is built up from two such simple compounds as carbon dioxide and water a large quantity of energy is expended, and so an equivalent amount is liberated when these carbohydrates break down. Since light furnishes the energy for the formation of carbohydrates we are now in a position to understand why it is so essential to the synthesis of the first products.

Synthesis is, however, not invariably dependent upon the supply of energy from external sources, since in some plants (*e.g.* Yeast, Bacteria) synthesis may be carried on by means of energy liberated internally as a consequence of exothermic chemical reactions (cf. pp. 341, 349).

The above generalised equation shows that in the production of carbohydrates in the green leaf oxygen is given off and that the volume of this latter is equal to that of the carbon dioxide taken in. The liberation of oxygen can be demonstrated by the following experiment (Fig. 128): A bunch of Canadian Pondweed or other water-plant (land-plants being unsuitable for this purpose) is placed in a cylinder of water (*c*) with the cut ends beneath an

inverted funnel (*f*), which is completely submerged and suspended as shown in the figure. A test-tube (*t*) full of water is inverted over the stem of the funnel and the whole apparatus is placed in bright light. Bubbles are seen to rise from the cut ends into the test-tube and, displacing the water, collect at the top; in this way after some hours a considerable quantity of gas is obtained. When all the water in the test-tube has been driven out, the usual glowing splinter test will show that the contained gas consists mainly of oxygen. If at the same time a similar apparatus is fitted up, except that water which has been boiled (and subsequently cooled) is employed, no liberation of oxygen will be observed, even in strong light. This is because in boiling all the carbon dioxide dissolved in the water was driven off, thus rendering photosynthesis impossible. The experiment also shows that aquatic plants depend on the carbon dioxide dissolved in the water for their photosynthetic process, a fact which is likewise apparent if we apply the iodine-test to the leaves of aquatics kept in boiled water.

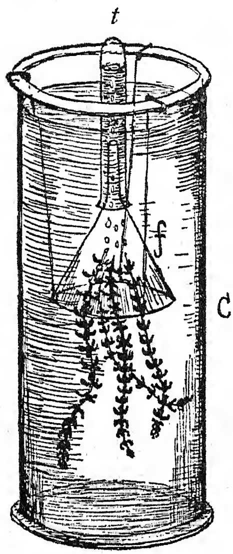


FIG. 128. Apparatus to demonstrate evolution of oxygen in a water-plant. For description, see text.

A modification of the above experiment enables us to investigate the influence of different conditions on the process of photosynthesis. For this purpose we use a single shoot of some water-plant, the cut end of which is covered with shellac varnish in which, on setting, a small hole is pricked. The shoot is loosely tied to a long glass rod, with the cut end upwards, and placed in a cylinder of water. In bright sunlight bubbles arise from the cut surface at a considerable rate, but their number is much diminished when the cylinder is placed in the shade and still more so in a poorly illuminated room, whilst in the dark there are practically none. Other things being equal, the rate of photosynthesis (as measured, for instance, by the number of bubbles per minute) thus decreases with the intensity of the light. The same method shows that it also diminishes as the temperature of the water is lowered and almost ceases when several lumps of ice are added. Increase of the amount of carbon dioxide present with the help of a siphon of soda-water demonstrates that the greater the amount of gas available, the more rapid is photosynthesis.

The factors affecting photosynthesis are thus the amount of carbon dioxide in the air, the supply of water, the intensity of the radiant energy, the temperature, the chlorophyll-content, and the structure of the leaf. These factors mutually affect one another, and the one which is nearest its minimal value sets a limit upon the rate of the process (cf. p. 519). For example, on a bright summer's day in the open the rate of photosynthesis is limited by the low concentration of carbon dioxide, as a consequence of which the light intensity, in many plants, might be diminished to about a third without a falling off of the rate of carbohydrate-formation.

The carbohydrates, together with nitrates, sulphates, and phosphates brought up in solution in the soil-water, are in part built up into the still more complex *proteins* and, as we have already seen (p. 207), the calcium and potassium salts play some part in their formation. It is a complex of proteins that constitutes the living protoplasm. The stages in the elaboration of proteins are still a matter of dispute, but they involve reduction of the oxidised form of nitrogen and sulphur as provided in the soil-solution.

The carbohydrates which do not undergo these changes are in part modified to form the *cellulose* of cell-walls, whilst the remainder are transferred from the leaf to other organs, where they are either used directly for growth or become stored up as a reserve. Carbohydrates are continually being thus conducted away from the seat of their formation, but on a bright day they are produced in photosynthesis more rapidly than they can be removed and consequently, towards the end of the day, many leaves exhibit an accumulation of transitory starch (p. 72) which, however, disappears again overnight. This transference of carbohydrates can be readily demonstrated by comparing the amount of the starch in a leaf removed at sunset and in one picked early the following morning. On the other hand, detached leaves with their petioles in water do not lose their starch during the night, since it cannot be removed. Proteins which are probably in large part built up in the leaves, since it is here that the materials for their production are chiefly found, are conveyed away in a similar manner.

The elaborated food-materials would appear to travel from one part of the plant to another mainly through the phloem. Interruption of this tissue, as in a ringing experiment (p. 199), seriously impedes transfer and is usually accompanied by an accumulation of food-material above the region of injury.

In contrast to the great constructive function of green (so-called *autotrophic*) plants, animals depend entirely on elaborated food-substances (*e.g.* carbohydrates, fats, proteins) and therefore obtain

their nutriment second-hand, either directly from the Vegetable Kingdom or indirectly (as in Carnivores) from other herbivorous animals; so that, if green plants were to disappear from the surface of the earth, almost the whole living universe would shortly perish.

There are plants, however, which are more or less dependent on elaborated food-substances and can only thrive when living or dead organic matter is available. Such plants, termed *heterotrophic*, comprise most of the Fungi and Bacteria, but also include a certain number of Flowering Plants in which the leaves are always of small size and usually devoid of chlorophyll. When part or all of the food is obtained from some other living organism the plant is known as a *parasite* and the organism on which it feeds as the *host*, whilst when the source of a plant's nourishment is non-living organic matter we speak of it as a *saprophyte*.

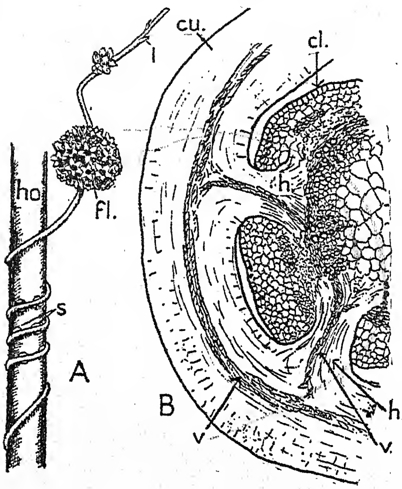


FIG. 129. Dodder (*Cuscuta*). A, small part of parasite, showing flowers (*fl.*), scale-leaves (*l.*) and haustoria (*s.*) attached to stem of host (*ho.*). B, *Cuscuta* (*cu.*)-stem cut longitudinally and host (Clover, *cl.*)-stem cut transversely, showing haustoria (*h.*) with vascular tissue (*v.*) joining that of host.

Among British Flowering Plants there are but few which are entirely parasitic, and none are very common; they include the Dodder, the Toothwort (see Fig. 131), and the Broomrapes. As a typical instance we may select the Dodder, a close ally of *Convolvulus*, which is an annual parasitic on many different hosts (*e.g.* Clover, Furze, Heather, etc.). The thread-like stem of this plant entwines the host (Fig. 129, A). Some of the coils are distant and unattached, whilst others are close together and bear the suckers (*haustoria*, *s*) through which nourishment is absorbed. There would appear to be no leaves, but careful examination discloses a number of minute scales (*l*) separated by long internodes and, as in all true parasites, completely devoid of chlorophyll. The stems vary in colour between bright yellow and red, and thus the plant becomes conspicuous, even before the rosette-like bunches of pink flowers (Figs. 129, A, *fl.*, and 130) are formed. By the production of plentiful small seeds the risk of a host not being found is

minimised, since one or other seed is very likely to germinate near a suitable plant.

The seedling is a simple thread containing a trace of chlorophyll, but showing no marked distinction into radicle, plumule, and cotyledons, *i.e.* the extreme reduction of the vegetative parts seen in the mature plant appears already in the seedling. The latter is, however, capable of a brief independent existence, and during this period the tip of the stem swings round in a circular manner and may thus happen to meet with a support; thereupon the root withers, so that the mature Dodder has no connection with the soil whatever. Failing the presence of a host the seedling soon dies away.

A striking feature of the anatomy of the Dodder is the feeble development of xylem, no doubt in relation to the reduction of the leaves. The *haustoria* arise from the stem (Fig. 129, B) as outgrowths (*h.*), which flatten out in contact with the surface of the host. The centre of the sucker grows out as a peg-like process, which penetrates the cortex and ultimately reaches the vascular tissue of the host, where it often expands considerably (Fig. 129, B, *h.*). At first this process consists of undifferentiated cells, but later those adjacent to the xylem become tracheids, whilst those in contact with the phloem develop as phloem-like elements. By the connection thus established between the conducting elements of host and parasite, the photosynthetic products and absorptive system of the former become available for the parasite.

The parasite, being relieved of those functions which necessitate elaboration of the vegetative structure, is enabled to utilise almost its entire energies for the purpose of reproduction. Simplification of structure, in every other direction but that which tends towards an increase in the output of seeds, is a marked characteristic of parasites. Even the ovules (cf. p. 445) and embryos are simpler in construction than those of most green plants, the material economised in this way presumably making possible a quantitative increase.

The Dodder is exceptional among British parasites, not only in being a climber and in having no roots in the mature condition, but also in being attached to the stem of its host. Nearly all other British plants of this kind are so-called *root-parasites*. They fix themselves by means of suckers to the roots of the attacked plant, as in the Toothwort (*Lathræa*) and the Broomrapes (*Orobanche*). The yellowish-white shoots of the former (Fig. 131) are usually found beneath the Hazel or the Wych Elm; they appear above ground in the early spring and flower about April. The overground part consists of an inflorescence of numerous purplish flowers, with

membranous leaves intermingled. At a varying depth beneath the surface of the soil one finds in the Toothwort a perennial stem which is extensively branched, the upturned tips constituting the annual aerial shoots. The whole underground system bears numerous decussate fleshy scales of a pink colour and richly branched adventitious roots which attach themselves to those of the host by flat suckers.

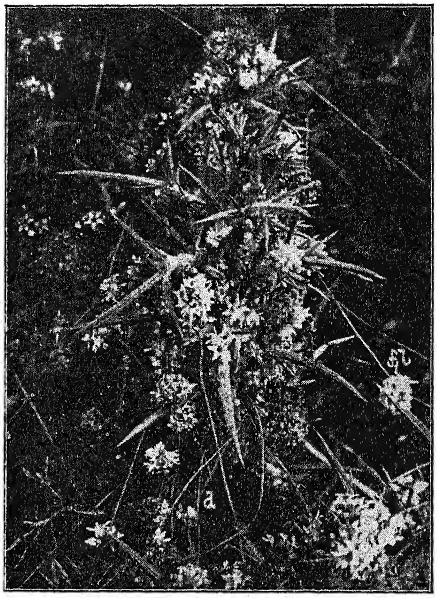


FIG. 130. Photograph of a portion of a plant of the Gorse, covered with the thread-like stems of the Dodder (*d*). On these the numerous bunches of flowers (*fl.*) can be seen. [Photo. E. J. S.]

Owing to the connection of the Toothwort with the extensive root-systems of its woody hosts and to the absence of the usual transpiring surface, an excess of water readily collects within the parasite. This excess is exuded from hydathodes (p. 195) lining the inner surfaces of the hollow fleshy scales borne on the underground stem, and at times the soil around the Toothwort appears quite wet. The hydathodes (Fig. 118, C, *h*) have the form of small domes consisting of living cells, viz. a large basal cell (cf. Fig. 118, B, *b.c.*) embedded in the epidermis, a short stalk-cell (*s.c.*), and a head composed of two to four cells lying side by side (Fig. 118, B, left-hand figure); in the middle of the head there is a small space between the cells, and above this the overlying cuticle is

pierced by a minute hole (*p.*) through which the water is secreted. Glandular hairs (Fig. 118, C, *g.h.*) of another type are present, which may take part in the secretion of water.

The species of Broomrape, the commonest of which is found on the roots of Clover, are close allies of the Toothwort and very similar in their overground organs. The seeds apparently germinate only when in contact with the roots of a suitable host. In

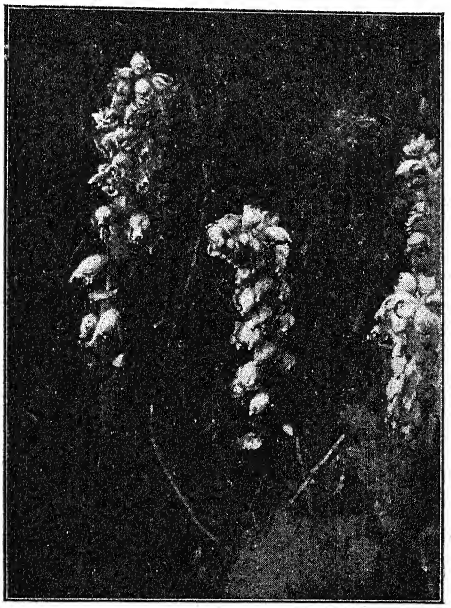


FIG. 131. Photograph showing three shoots of the Toothwort; each bears numerous flowers. [Photo. E. J. S.]

common with all other parasites, the Broomrapes exhibit a much reduced leaf-surface and numerous minute seeds dispersed by wind, but even so these plants are by no means frequent. The reduction of the vegetative as compared with the seed-producing part has gone much farther in some tropical parasites, in which the vegetative organs are represented by one much-branched haustorium traversing the tissues of the host (e.g. *Rafflesia*).

The Mistletoe is a somewhat exceptional type of parasite found growing on the branches of Apple, Hawthorn, etc. It possesses green leaves and is thus a *semi-parasite*. It sends peg-like suckers (whose growth in length keeps pace with the secondary thickening of the branch) deep down into the wood of the host. It differs from most other British plants, not only in its parasitic qualities,

but also in growing aloft on the branches of trees. This kind of situation is, however, frequented by many non-parasitic plants of the Tropics (*e.g.* Orchids, p. 111).

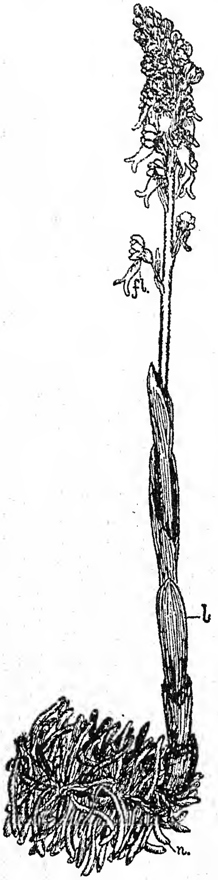


FIG. 132. Complete plant of the Bird's-nest Orchid (*Neottia*) (about two-thirds natural size). *fl.*, flower; *l*, leaf; *n*, the underground nest-like portion.

The commonest saprophyte amongst British Flowering Plants is the Bird's-nest Orchid (*Neottia*) found growing in Beech-woods. This saprophyte (Fig. 132) blooms in late May, the plant emerging from the humus as an unbranched stem bearing a few scaly leaves (*l*) of moderate size and numerous flowers (*fl*), all of a brown colour, little or no chlorophyll being present. The erect shoots are borne on a subterranean mycorrhizal portion (*n*) (cf. p. 110), the numerous branches of which are interwoven so as to form a structure somewhat resembling a bird's nest; hence the common name. The saprophyte thus obtains its nourishment from the organic matter in the humus with the aid of the contained Fungus (Fig. 63, *m*).

Although parasites and saprophytes are rare amongst Flowering Plants, all Fungi and most Bacteria depend on these methods of nutrition and are often responsible for processes of decay (p. 335). An association with Fungi is, however, not confined to saprophytes like *Neottia*, but is seen in many other higher plants (*e.g.* the Conifers, the Beech, and most members of Ericaceæ), all of which grow where humus is plentiful. The threads of the Fungus often form a complete investment to the young parts of the root-system and thus constituting a mycorrhiza (p. 110), not only take over the water-absorbing functions of the root-hairs (which are absent in such plants), but also no doubt aid in the taking up of organic matter from the humus. The Fungus, like the higher plant, probably derives nourishment from this association. In some plants (*e.g.* Heather) the mycorrhizal relationship appears to be obligatory, whilst in others the presence or absence of fungal threads in the roots does not seem to affect the vigour of the Flowering Plant. The association of Fungus and higher plant can be regarded as a form of

controlled parasitism and under certain conditions the balance may be disturbed and the Fungus become harmful.[1]

An association between roots and Bacteria is met with in most members of the Leguminosæ. On digging up a plant of the Bird's-foot Trefoil or a Vetch we find that the roots bear a number of small swellings (Fig. 133, *t*), the so-called *root-nodules*, in which the Bacteria occur.

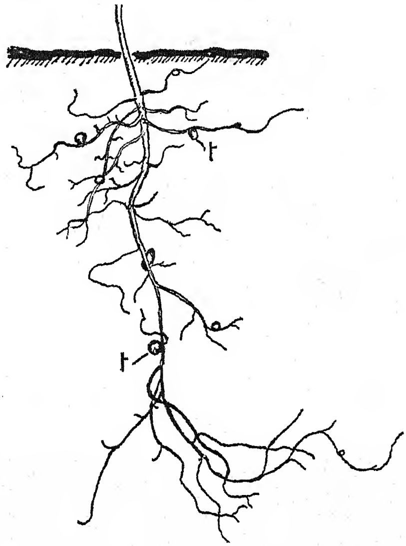


FIG. 133. Root-system of the Meadow Vetchling (*Lathyrus aphaca*), showing the root-nodules (*t*) (natural size). The level of the soil is indicated by a heavy line.

Even in the time of the Romans the inclusion of Leguminous plants in a rotation of crops was recognised as beneficial. Experience has shown that cultivation of Clovers, Sainfoin, Lucerne, etc., materially increases the nitrogen-content of the soil, especially if the crop is subsequently ploughed into the field (so-called green manuring). This phenomenon remained unexplained until it was discovered that the swellings upon the roots of Leguminous plants are inhabited by Bacteria (*Bacillus radicicola*, Fig. 227, *f*; cf. p. 421), capable of fixing free nitrogen, and present in every healthy soil. Infection of the root takes place through the root-hairs, probably at a phase when the organism is capable of free movement; having penetrated the root-hairs, the Bacteria pass into the adjoining cells, which are thereby caused to divide, so that a gall-like structure arises. Within the cells of this nodule rapid multiplication of the Bacteria ensues, probably at the expense of carbohydrates furnished by the Leguminous plant. At the same time, however, the latter profits by the nitrogenous material formed by the Bacteria, the removal of which is indeed necessary for their continued activity. In the mature condition large numbers of the Bacteria, within the cells of the nodules, assume an irregular form, and become digested by the action of the host. A limited number persist unaltered, and return to the soil as the roots decay away.

[1] For further details, see M. C. Rayner, *Mycorrhiza*. Wheldon & Wesley, 1927 (246 pp.).

The relation between the nodules and these nitrogen-fixing Bacteria is shown by the fact that Leguminous plants, grown from seed in soil which has been thoroughly sterilised by heating, fail to develop any nodules, and are just as dependent on a supply of soil-nitrates as other green plants. It appears that different strains of these Bacteria infect different Leguminous plants, and that normally those of a particular strain only attack other individuals

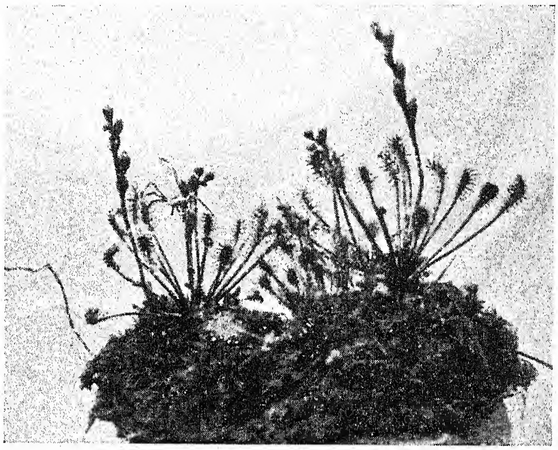


FIG. 134. Photograph of two plants of the Sundew (*Drosera*). On one of the leaves of the left-hand plant an insect (*ins.*) has been caught. *bl.*, leaf-blade; *infl.*, inflorescence; *p*, petiole. [Photo. E. J. S.]

of the same species. Similar nodules of a larger size occur on the roots of the Alder and the Bog Myrtle (*Myrica*).

Another special method of nutrition is that of the so-called *insectivorous plants*.[1] A common example is the Sundew (Fig. 134) which frequents boggy situations, such as damp moorlands and peaty heaths. The plant consists of a radical rosette of reddish leaves with relatively long petioles (*p.*), expanding into a blade (*bl.*) which is rounded or oval according to the species; from the centre of the rosette arise one or more upright inflorescences (*infl.*) with white flowers. The upper surfaces and the edges of all the leaf-blades are beset with numerous secretory tentacles having swollen ends which glisten owing to a sticky covering (see Fig. 134). These tentacles are supplied with a vascular bundle which extends into the enlarged tip. In the latter the bundle is enveloped by three distinct layers of cells, of which the innermost is thickened after

[1] See also C. Darwin, *Insectivorous Plants*. John Murray, 1908 (377 pp.).

the manner of an endodermis, while the two outer layers which contain the crimson pigment are those actually concerned in secretion; the superficial one has a palisade-like structure.

Insects attracted by the tentacles alight on the leaf and adhere to the secretion. Unless the insect be powerful enough to escape, the tentacles touching it begin to bend slowly towards the middle

FIG. 135. Photograph taken from above, showing the leaf-rosettes of a considerable number of plants of the Butterwort (*Pinguicula*). At the top left-hand corner is a specimen of the Cross-leaved Heath (*Erica tetralix*) and on the right, near the top, the trailing shoots of the Bog Pimpernel (*Anagallis tenella*). [Photo. E. J. S.]

of the blade, and this is soon followed by a similar movement of the others.

In this way the insect's body is firmly held against the surface of the leaf, in fact it is often completely hidden from view by the incurved tentacles. At this stage digestive juices pass out from these structures and, attacking the insect's body, slowly convert its soft parts into a soluble form when they are absorbed by the tentacles. After a considerable lapse of time the latter resume their normal position and now the undigested hard portions of the insect alone remain. The Sundew is able to live without such insect-food, but under these circumstances it produces fewer flowers and seeds—in other words, its vigour is much diminished.

The Butterwort (Fig. 135) captures its prey in a somewhat similar manner. Here the upper surfaces of the yellowish radical leaves bear numerous sticky digestive glands (Fig. 136, *d*) composed

of a basal cell, a short stalk-cell, and a usually eight-celled head. Similar glands occur also on the under-surface, but these are probably mainly concerned with the excretion of water. The digestive glands are accompanied by other long-stalked glands (*m.*), whose umbrella-like heads secrete the sticky mucilaginous matter to which the insects adhere.

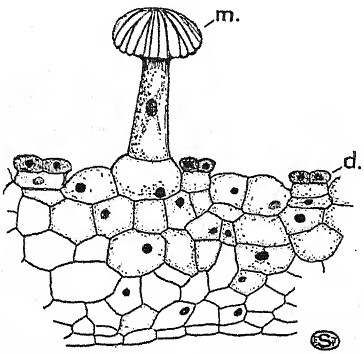


FIG. 136. Transverse section through a small part of the leaf of the Butterwort (*Pinguicula*), showing the short digestive glands (*d.*) and a mucilage-secreting hair (*m.*).

A peculiar instance is afforded by the Bladderwort, a submerged water-plant bearing numerous little sack-like structures on its deeply divided leaves (Fig. 137, A, *bl.*). Each of these bladders has a narrow aperture (Fig. 137, A, *o*) surrounded by hairs and closed by a trap-door opening only inwards (Fig. 137, B, *t*). The inner surface of the bladders bears four-armed hairs and absorbs the internal liquid. When the trap-door is shut this absorption leads to contraction of the bladder under tension. If a minute aquatic animal comes in contact with certain of the hairs around the aperture, the trap-door is released and water rushes in, carrying the organism with it. The imprisoned animals ultimately die, and the products of their decay are absorbed with the surrounding fluid so that a state of tension again arises. No digestive enzyme is known to be secreted by this plant.

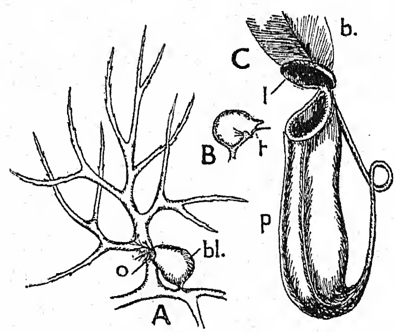


FIG. 137. A, Single leaf of the Bladderwort (*Utricularia*) (about three times the natural size). B, Single bladder of the same cut through lengthwise (same scale as in A). *bl.*, bladder; *o*, aperture of bladder; *t*, lid of bladder. C, Single pitcher of the Pitcher-plant (*Nepenthes*) (somewhat reduced). *b*, leaf-like broadening of base of petiole; *l*, lid; *p*, pitcher.

Mention should also be made of the well-known Pitcher-plant (*Nepenthes*), in which the blade is modified to form the pitcher (Fig. 137, C, *p*), whilst a broadening (*b*) of the lower part of the petiole fulfils the usual functions of the lamina; the rigid lid

(*l*) protects the contents from being flooded by rain. Numerous overlapping waxy flakes are secreted on the smooth inner surface of the pitcher, so that insects cannot obtain a foothold and slip into the liquid, which occupies the lower part; they are prevented from crawling out by the numerous downwardly directed scales upon the wall. Subsequently their bodies undergo digestion as a result of secretion from short-stalked glands. These are provided with a robust oval head of palisade-like cells and are situated beneath the overhanging scales in the lower part of the pitcher. The products are absorbed by the plant.

Most insectivorous plants frequent swampy localities, and it is probable that by their special method of nutrition they make up for the deficiency in nitrogenous salts which often obtains in such habitats.

Our study of the nutritive processes in autotrophic plants has shown that green leaves are the world's great factories, which build up complex from simple substances and store up the radiant energy of the sunlight in a form available for the maintenance of the plant's activities. More food is often elaborated than is necessary for immediate requirements and the surplus is stored up for a twofold purpose. For, such food-reserves not only further new growth by supplying materials to sprouting buds in the spring, but also enable the parent-plant to provide the necessary start in life for its offspring, whether these arise from seeds or from organs of vegetative propagation.

CHAPTER XX

FOOD-STORAGE AND VEGETATIVE REPRODUCTION

MANY plants are specially fitted for vegetative reproduction, namely, propagation by detachment of some part of the vegetative organs. One of the great advantages of the creeping habit is the

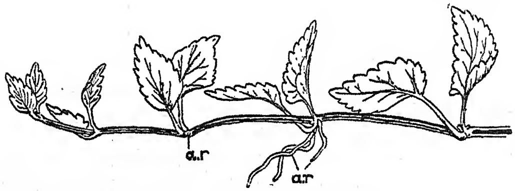


FIG. 138. Creeping shoot of the Yellow Dead-nettle (*Galeobdolon*) (about half natural size). The upright flowering axis from which this shoot arises is not shown. *a.r.*, adventitious roots, fully developed at one node, as rudiments at another.

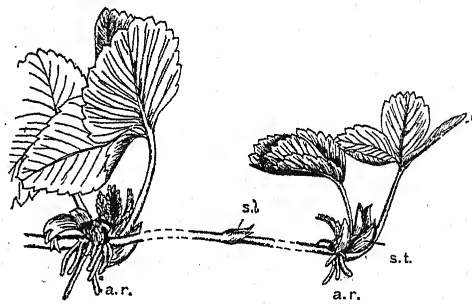


FIG. 139. Runner of the Strawberry (*Fragaria*, about half the natural size). One plant produced from a runner is seen on the left, a younger one on the right. The full length of the runner is by no means indicated. *a.r.*, adventitious roots; *s.l.*, scale-leaf; *st.*, stipule.

rapidity with which a considerable surface of the ground is covered (cf. p. 15). Tufts of adventitious roots are produced from some of the nodes of the prostrate shoots (e.g. *Lysimachia nummularia* and Ground Ivy, Fig. 7), and thus, if the older parts die away, the

rooted branches become free as independent units. A similar propagation by horizontal creeping shoots, which arise from the base of the erect flowering stem and subsequently lose their connection with the main plant, is seen in the Yellow Deadnettle (Fig. 138).

Such creeping shoots often take the form of *runners*, as in the Cinquefoil (*Potentilla reptans*) and the Strawberry (Fig. 139). Towards the end of the flowering season numerous slender branches arise from the axils of the radical leaves of the Strawberry and radiate over the surface of the ground. These runners elongate with great rapidity, forming a few small scale-like leaves (*s.l.*) separated by long internodes; new plants are ultimately produced from the upturned tips of the runners, whilst the latter are continued by axillary branches, each arising from a leaf of a new rosette, giving a sympodial construction. Adventitious roots (*a.r.*) grow out from the base of the new plant and sooner or later the connecting portion of the runner decays away. The runner is distinguished by its considerable elongation, which serves to diminish competition with the parent.

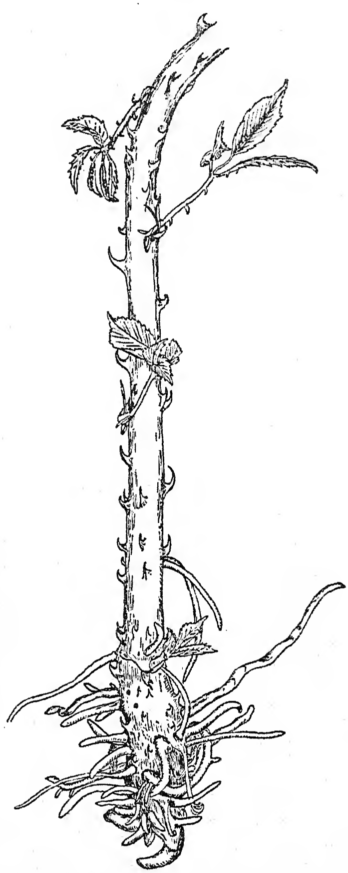


FIG. 140. Rooting branch of the Bramble (*Rubus*) with numerous adventitious roots arising from the tip and showing one of the small leaves from which axillary shoots are produced (about two-thirds natural size).

A special method of vegetative reproduction by overground shoots is seen in the Bramble (Fig. 140), in which some of the woody stems arch over towards the ground and, on reaching the latter, exhibit a swelling of their tips from which numerous adventitious roots are produced. From the axils of small leaves, which occur intermingled among the roots on the overground part, leafy shoots develop and produce a new Bramble-bush which after a few years becomes independent.

The *suckers* found in some fruit-trees (*e.g.* Damson), as well as in the Poplar and the Yarrow (Fig. 141), are axillary underground shoots which sooner or later come above the surface, when their tips give rise to new plants that remain connected with the parent for some years. As a consequence of this prolonged attachment the daughter-plant is nourished by the parent until it becomes fully established; hence suckers are not swollen out with food-reserves like other subterranean organs of vegetative propagation,

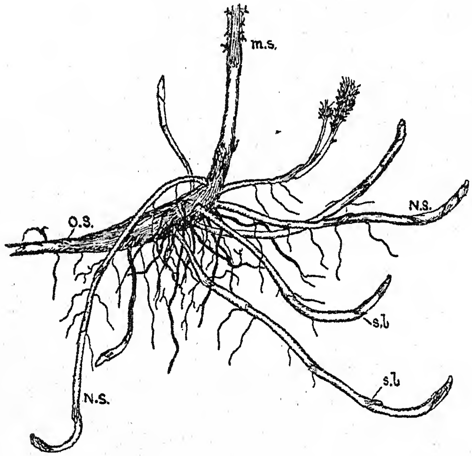


FIG. 141. Base of a plant of the Yarrow (*Achillea*), showing the remains of an old sucker (*o.s.*), whose upturned tip produced the main stem (*m.s.*), and numerous new suckers (*n.s.*) (about two-thirds natural size). *s.l.*, scale-leaves.

to be subsequently considered, in which separation from the parent takes place before the daughter-plant is self-supporting. The underground portion of the sucker is white, but is readily distinguished from a root by the scale-leaves (*s.l.*) borne upon it. Here, too, the construction is sympodial, the main axis for any season being a lateral branch of that of the previous season (cf. Fig. 141).

Vegetative reproduction may be accomplished by adventitious shoots arising, usually endogenously, from roots, as in the Elm. It is this feature which renders the Bindweed, the Creeping Thistle (*Cnicus arvensis*), and the Sheep's Sorrel (*Rumex acetosella*) such obnoxious weeds, and the Horse Radish so difficult to eradicate.

In many plants a portion of the stem is situated beneath the surface of the soil, such underground stems when they creep horizontally being termed *rhizomes*, whilst the short more or less erect structures seen in the Buttercup and Primrose are known as

root-stocks. The Iris possesses a rhizome which is a thick branched horizontal stem bearing foliage leaves towards the tips and the remains of leaves attached to the leaf-scars on the older portions. The Solomon's Seal shows a further specialisation. Here the aerial flowering shoots will be found to arise vertically from a thick white rhizome (Fig. 142), situated at some depth in the soil and covered with ring-like remnants of reduced scale-leaves (*s*), as well as with adventitious roots (*a.r.*) which occur principally upon the under side. Examination of an entire plant in spring shows that the ends of the main axis of the rhizome and its branches curve up to form the overground shoots (*a.s.*), whilst a bud, from the axil of the lowest scale-leaf on the latter, continues the horizontal growth of the sympodial subterranean system.

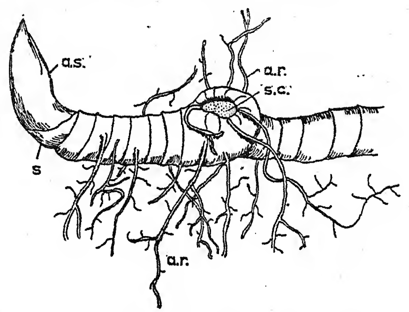


FIG. 142. Rhizome of the Solomon's Seal (*Polygonatum*) in autumn (about half the natural size). *a.r.*, adventitious roots; *a.s.* bud of next year's aerial shoot; *s*, scale leaves on rhizome; *sc.*, scar of aerial shoot of past season. The portion of the rhizome to the right of this scar was formed a year earlier than the part to the left of it.

Some time after flowering the aerial shoots die away leaving on the upper surface of the rhizome a large round scar (*sc.*), the so-called "seal," marked by numerous dots which represent the broken ends of the vascular strands. In the autumn (the stage shown in the figure) the buds developed from the base of the aerial shoots have completed their horizontal growth, and their tips have now curved upwards, ready to grow above the soil in the following season. The rhizome persists for some time, so that several seals marking the annual flowering shoots may be found along its length, but sooner or later the older parts decay and as a consequence the branches become separate plants. Owing to food-reserves in the rhizome, the aerial shoots grow rapidly in the spring and the detached branches are well equipped for an independent existence.

The rhizome of the Solomon's Seal therefore serves not only as an organ of vegetative propagation, but also for food-storage, and thus constitutes the means of persistence for this perennial from year to year (cf. p. 12). Similar examples are furnished by the Lily of the Valley (*Convallaria*) and many Grasses, in which the terminal buds are encased in scales whose tips form a hard point, well suited to pierce the ground (seen also in the Sand

Sedge, *Carex arenaria*). The slender underground stems of such plants as the Woodruff (*Asperula*) serve mainly for extension and, in common with many other rhizomatous plants, the Woodruff exhibits a gregarious habit. It is this gregarious habit that accounts for the unisexual (cf. p. 449) patches of such plants as

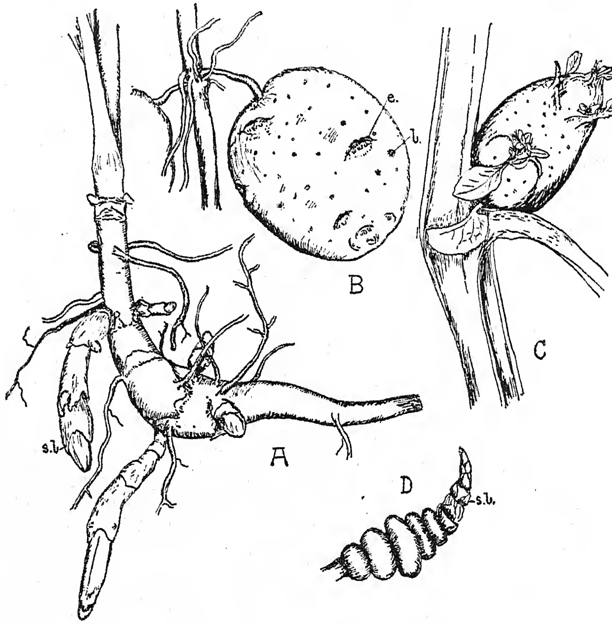


FIG. 143. Food-storage in tuberous stems (all figures about two-thirds natural size). A, Perennial Sunflower. B, Potato (normal). C, Potato-tuber formed in axil of leaf of aerial shoot. D, Chinese Artichoke (tuber only). *e*, "eyes"; *l*, lenticels; *s.l.*, scale-leaves.

the Nettle and Dog's Mercury, each patch being derived from one individual which has spread vegetatively.

Vegetative reproduction is likewise combined with food-storage in the Perennial Sunflower (*Helianthus perennis*, Fig. 143, A), the Jerusalem Artichoke (*Helianthus tuberosus*), and the Chinese Artichoke (*Stachys tubifera*, Fig. 143, D), in all of which a number of axillary branches arise from scale-leaves on the underground part of the stem, in the course of the summer, and grow more or less horizontally through the soil. These shoots bear scale-leaves (*s.l.*) showing the same decussate arrangement as the foliage-leaves. The food formed by the aerial shoot is in part stored up in the more or less swollen tips of the subterranean branches, and, after the

plant has died down in the autumn, the latter become detached, giving rise to new and independent plants in the following spring; each of these thus really represents a lateral branch of the plant of the previous season. In the Chinese Artichoke (Fig. 143, D) the swollen tips exhibit a succession of swellings, each representing an internode, whilst in the Jerusalem Artichoke the several internodes form a large tuber of irregular shape. The abundant food-materials stored up in these organs render them valuable as vegetables.

The *tubers* of the Potato are formed in the same way, but differ in having a protective covering of cork (the peel), pierced by lenticels (Fig. 143, B, *l*). The "eyes" (*e*), which are best seen on young tubers, represent scale-leaves with axillary buds; sometimes the Potato is cut up into pieces, each including an "eye," which thus serve as the starting-point for as many new plants. Under exceptionally favourable conditions some of the axillary buds on the overground parts of the plant occasionally develop into similar tubers (Fig. 143, C) and here the true character of the scale-leaf and axillary bud is very obvious.

The *corm* of the Crocus is a special kind of root-stock formed by a swelling up of the base of the flowering stem. If we halve the lower part of a plant in April, as in Fig. 144, D, the new corm (*c. 1914*) is seen arising as a swollen structure enclosed within the sheathing bases of the lower leaves of the flowering shoot (*a.s.*), whilst below it is the corm (*c. 1913*) from which the latter has arisen. Later in the season, when the flowering shoot has withered, the new corm will be found to have increased greatly in size, the old one having shrivelled considerably, so that it is now the smaller of the two. In the autumn the corm has attained its full dimensions, is enveloped in the brown tunic constituted by the remains of the sheathing leaf-bases of last spring's shoot, whilst in their axils one or more buds (Fig. 144, B, *b*) have developed; beneath it is a dark mass, the remnant of the old corm (cf. Fig. 144, A and D, *c. 1912*).

The corm is thus a much-swollen stem-base ensheathed in scales and bearing one or more axillary buds, in each of which the young leaves and flower for next year's growth (Fig. 144, C) can be recognised. On removing the scales it will be found that each of them is attached around the whole circumference of the corm (Fig. 144, B, *sc.*), whilst at the top of the latter the scars left by the withered flowering stem and foliage leaves can be distinguished. In the following season the buds grow out to form the overground shoots and at the base of each of these the same sequence is repeated (Fig. 144, A and D). It will be realised that the corms

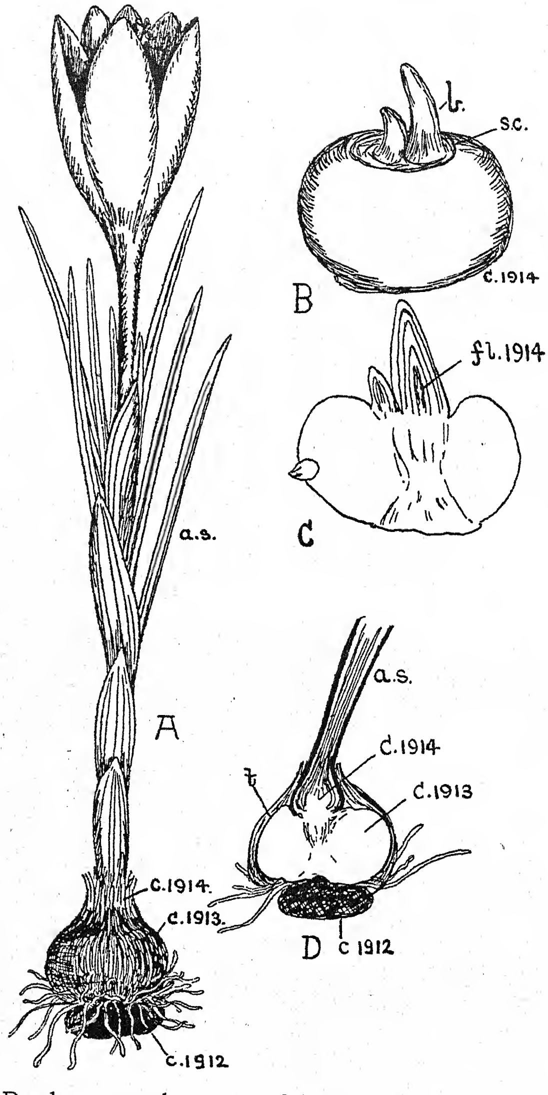


FIG. 144. Development and structure of the Crocus-corm. A, Spring condition. B, Winter condition, showing two buds which will produce flowering shoots in the subsequent season; one of the scales has been removed near the top of the corm, leaving a ring-shaped scar (*sc.*). C, Longitudinal section of the corm at the stage shown in B; all scales removed. D, Longitudinal section of base of corm and flowering shoot at stage shown in A. (All figures about natural size.) *a.s.*, aerial flowering shoot; *b.*, buds for next season's flowering shoots; *c. 1912*, *c. 1913*, *c. 1914*, corms of successive years; *fl. 1914*, flower which will unfold in 1914; *t*, tunic.

of any given year are lateral to those of the previous year, so that the branching of the Crocus-plant is sympodial, each new segment being terminated by a flower. Inasmuch as the corms usually bear several buds and each of these gives rise subsequently to a separate daughter-corm, extensive vegetative reproduction is carried on.

The underground corm of the Cuckoo-pint is an abbreviated and stout rhizome, in which the growths of previous years do not die away so rapidly (Fig. 145). In the autumn we find a well-developed leaf-bud for next year's growth, the base of which is

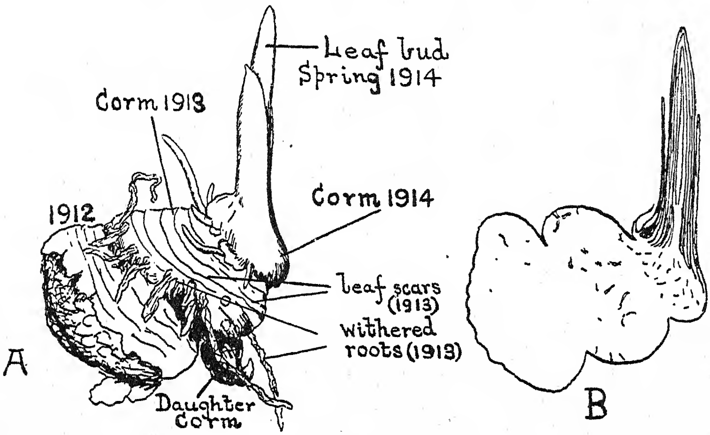


FIG. 145. Corm of the Cuckoo-pint (*Arum maculatum*) in autumn (natural size). A, Entire. B, In longitudinal section.

already prominently swollen to initiate the corm which will be completed in the subsequent season (corm 1914 in Fig. 145, A), whilst behind it are one or more corms of previous years (corm 1913, 1912) on which the ring-like leaf-scars and remains of roots are a prominent feature. The analogy to a fleshy rhizome, such as that of the Solomon's Seal, is very clear, the construction again being sympodial. Corms are also found in the Bulbous Buttercup (*Ranunculus bulbosus*).

Bulbs, such as those of the Tulip, Onion, or Narcissus, consist of a number of fleshy scale-leaves (Fig. 146, A, *fl.sc.*) encircling one another and the central bud (*f.a.*), the whole arising from a flat disc-like stem (*st.*) and surrounded by a thin brown papery investment (*i*) of one or more scales. The detailed structure of bulbs, however, differs considerably in various plants. In a halved Tulip-bulb we can recognise the central bud, comprising the future flower and several young foliage-leaves, and just within the flattened

base the rudiments of numerous adventitious roots (*a.r.*) appearing as small lines at right angles to the surface. In the axils of one or more of the fleshy scales will be found minute buds (*d.b.*), which will give rise to the new bulbs for the following season's growth. When the bulb begins to sprout, the adventitious roots exhibit a rapid growth (Fig. 146, B, *a.r.*) and, after they have become well established in the soil, the central bud elongates carrying up the foliage-leaves and the terminal flower which soon expands. This

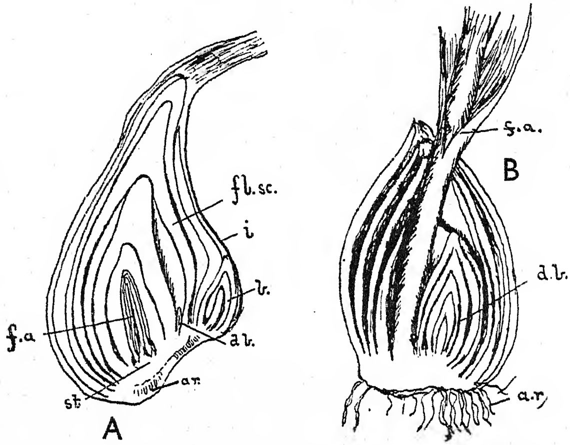


FIG. 146. Structure and development of bulb of Tulip (natural size). A, Winter condition in longitudinal section. B, Spring condition in longitudinal section, only the base of the flowering axis being shown. *a.r.*, adventitious roots; *b*, incompletely developed daughter-bulb; *d.b.*, bud which is giving rise to a daughter-bulb; *f.a.*, flowering axis; *fl.sc.*, fleshy scales of bulb; *i*, investment of dry scales; *st.*, flattened stem.

growth takes place at the expense of the food-substances stored up in the bulb-scales which consequently commence to shrink (cf. Fig. 146, B).

After flowering, the green foliage-leaves, as in the Crocus and Cuckoo-pint, persist for a considerable time; during this period the food formed by them is passed down into the axillary buds of the bulb, which now exhibit a rapid increase in size (Fig. 146, B, *d.b.*). The latter also receive any surplus food-material from the main bulb. When the overground shoot withers, we consequently find that the original bulb has been replaced by one or more daughter-bulbs which have developed from the axillary buds and are enclosed in the shrivelled papery remnants of the parent-bulb. Since the main axis of the latter is terminated by a flower, the new Tulip-bulbs are axillary branches. When there are

several daughter-bulbs, the supply of food is sometimes not sufficient for an adequate development of all, and some of them consequently appear as small structures adhering to the surface of the larger ones (Fig. 146, A, *b*). It will be realised that the

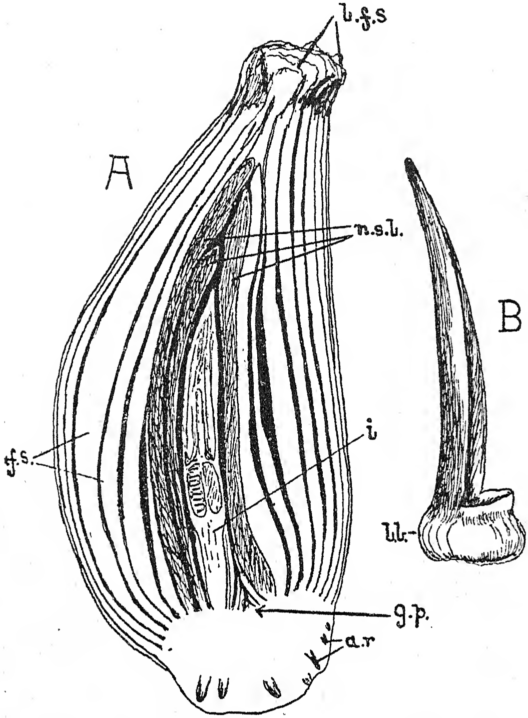


FIG. 147. Structure of bulb of *Narcissus* (somewhat enlarged). A, In longitudinal section. B, Single foliage-leaf from the latter, showing the sheathing leaf-base. *a.r.*, adventitious roots; *g.p.*, meristem of bulb (*i.e.* apex of stem); *i*, inflorescence; *l.b.*, leaf-base which enlarges to form a bulb-scale in the next season; *l.f.s.*, enlarged bases (scales) of leaves of previous seasons; *n.s.l.*, young foliage-leaves of current year, whose bases will form fleshy scales in the next season.

bulbs of the Tulip are really nothing more than huge buds in which most of the bud-scales are swollen with stores of food-material.

The bulbs of *Narcissus* (Fig. 147) or Snowdrop (*Galanthus*) are of a different type. The fleshy scales of the bulb (Fig. 147, A, *l.f.s.*) here consist mainly of the swollen bases of foliage-leaves of preceding seasons (of the last year only in the Snowdrop, of several years in the Narcissus). The foliage-leaves (*n.s.l.*) arise from the

disc-like stem, while the flowering shoot (*i*) develops in the axil of one of them. The terminal bud (*g.p.*) of the main axis is recognisable at its side and persists from year to year, producing each season two or more foliage-leaves and an axillary inflorescence, the whole enveloped in a membranous sheath; the bases of the leaves, as well as this sheath, swell up after flowering to form new fleshy scales for the next season's bulb. Other buds may be formed in the axil of the outermost scale and give rise to daughter-bulbs, whereby multiplication is effected. It will be noted that the growth of the Narcissus-bulb takes place in a monopodial manner, whilst that of the Tulip is sympodial. The bulb of the Wild Hyacinth agrees with the Tulip in its sympodial construction, but with the Narcissus in consisting mainly of swollen bases of foliage-leaves.

Vegetative propagation is also seen in the formation of so-called *bulbils*, *i.e.* small buds which become readily detached and the leaves of which, as in bulbs, are filled with food-reserves. In the British flora the best example is the Wild Onion, where the bulbils replace flowers. The Lesser Celandine reproduces by bulbils which consist of an axillary bud bearing swollen adventitious roots.

Vegetative reproduction is widespread among Flowering Plants, and even more abundant among lower forms of plant-life in which, moreover, it often takes place with great rapidity. As contrasted with seed-production, the advantage of vegetative propagation lies in its simplicity, no complex union of cells being necessary such as is involved in the formation of a seed (cf. p. 469). Vegetative reproduction, however, usually fails to bring about a wide separation of the offspring, which develop side by side and may thus mutually harm one another by competition, although in propagation by runners or underground branches this disadvantage is minimised.

All the storage-organs considered in this chapter are found at a certain distance beneath the surface, the exact depth appearing to be relatively constant in the same soil for each kind of plant. When such forms arise from seed, the seedlings are at first situated near the surface, but they are gradually brought to the appropriate depth by the agency of so-called *contractile roots* (*e.g.* in the Cuckoo-pint and Hyacinth). These are thick structures (Fig. 148, B and C) arising from the under side of rhizome, corm, or bulb, and penetrating downwards into the soil. After their lower portions have become firmly anchored the upper parts (viz. those nearest the parent organ) shorten, their surface becoming markedly wrinkled. This is due to a change in form of the cortical cells which, while contracting longitudinally, expand laterally. As a consequence the structure from which the roots arise is dragged down to a lower level. Such contractile roots are produced each season until the

correct depth has been attained. Sometimes (*e.g.* the Crocus, Fig. 148, B) the new individuals (*d.c.*) arise on the top of the old ones (*m.c.*) and so come to lie higher in the soil; in these the level is adjusted by contractile roots (*c.r.*) formed at the beginning of each season on the daughter-individuals. Rhizomes maintain

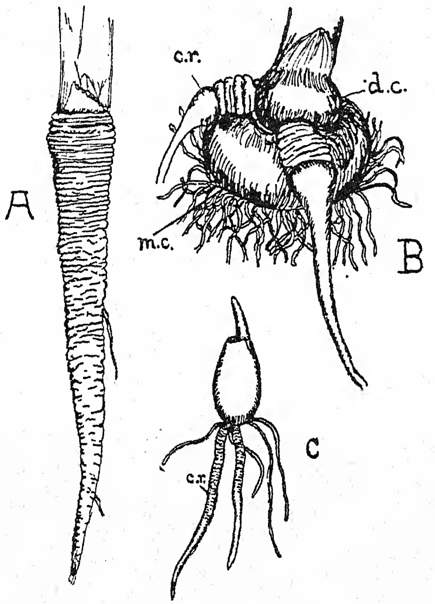


FIG. 148. Contractile roots (A and B, natural size; C, slightly enlarged). A, Tap-root of Fennel (*Fœniculum*). B, Crocus-corm. *c.r.*, contractile root; *d.c.*, daughter-corm; *m.c.*, mother-corm. C, One-year-old bulb of Broad-leaved Garlic (*Allium ursinum*) with contractile roots (*c.r.*).

their appropriate depth by changes in the direction of growth. The so-called droppers of the Tulip likewise serve to adjust the level of the daughter-bulbs.

Contraction is also exhibited by the swollen roots (p. 113) of the Dandelion, Dock, Fennel (Fig. 148, A) and other members of the Umbelliferæ. The new leaves of the radical rosette formed above the old ones at the beginning of each season are thus pulled down in close contact with the soil.

CHAPTER XXI

THE PHYSIOLOGY OF RESPIRATION[1]

THE life-processes of every living organism are always associated with a chemical break-down, the outward evidence of which is an absorption of oxygen and an emission of carbon dioxide. This respiration goes on at all times in the plant, but is masked during the daytime by the more active photosynthetic process in which the gaseous exchange is reversed. As a consequence the volume of oxygen evolved by the plant is less than that actually formed in photosynthesis, since part of it is used for respiration; similarly, the carbon dioxide produced in the latter process is not liberated, when the plant is exposed to light, owing to its being used for purposes of photosynthesis as soon as it is formed. Hence an evolution of carbon dioxide from a green plant can only be demonstrated in darkness.

It is probably for the most part carbohydrates that are broken down in the process of respiration and, taking grape sugar as an example, we can in a general way illustrate the very complex chain of chemical changes involved by the following equation:—

$$\underset{\text{Grape sugar.}}{C_6H_{12}O_6} + \underset{\text{Oxygen.}}{6O_2} = \underset{\text{Carbon dioxide.}}{6CO_2} + \underset{\text{Water.}}{6H_2O} + 674 \text{ calories}$$

The volume of carbon dioxide given out is therefore equal to that of the oxygen taken in, and water-vapour is simultaneously produced. Evolution of water-vapour in the course of the breathing process is a familiar fact in animals, but is difficult to demonstrate in plants owing to the simultaneous occurrence of transpiration.

A method of demonstrating the necessity of oxygen for growth was described on p. 9. That plants in breathing remove a constituent of the air can be shown by placing germinating Peas in a flask which is closed with an air-tight rubber cork fitted with a

[1] For reference-books, see the general works on plant physiology cited on p. 193; also W. Stiles and W. Leach, *Respiration in Plants*. Methuen, 1932 (124 pp.).

glass tube bent as in Fig. 149. Suspended in the flask by a cotton thread is a small bottle (*b*) containing a concentrated solution of caustic potash, whilst the free arm of the tube dips into a tumbler of water. Or a better method is to suspend the Peas in a small basket of wire-gauze and to cover the bottom of the flask with soda-lime. In either case the carbon dioxide evolved by the Peas, in place of the oxygen taken in, is absorbed by the potash or soda-lime, and as a consequence a reduced pressure is produced within the flask, so that a column of water rises in the tube, as shown in the figure. To avoid the effect of changes in temperature the flask as a whole can be placed in a large vessel of water which should preferably be maintained at a constant temperature.

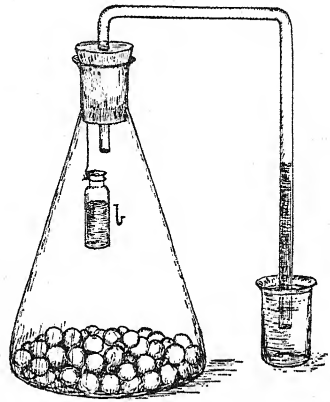


FIG. 149. Apparatus to demonstrate that germinating Peas give off carbon dioxide in the process of respiration. For description, see text.

Since every living cell must breathe, there must be free access of oxygen to all parts, and this is effected by the continuous system of air-spaces opening to the exterior by the stomata (p. 152) and lenticels (p. 189). To illustrate the continuity of the whole intercellular space system of the plant and its connection with the stomatal apertures we use the apparatus already described on p. 199 (Fig. 122, B). Two similar leafy shoots of a plant in which the stomata are confined to the lower side of the leaf are selected. In the one the under surfaces, in the other the upper surfaces of the blades are vaselined, after which the shoots are attached to the free ends of the glass tubes (in the way shown in Fig. 122, B), so that the cut end of the former extends into the latter above the level of the surrounding rubber. Prior to doing this the long arm of each tube is partially filled with a column of water extending some 4 to 6 inches above the end of the stem. When the flask is cooled a stream of air-bubbles begins to arise from the cut end of the shoot in which the upper sides of the blades had been vaselined, and to ascend through the column of water in the long arm of the tube; this may go on for several hours as the flask becomes cooler. From the other stem, however, few or no bubbles arise.

The fact that the lenticels are apertures giving access to the intercellular system can be shown by placing woody twigs, in

which the cut ends have been sealed with melted paraffin-wax, in warm water, when large bubbles of air will be seen to arise from the lenticels. If the stem of a plant is cut off just above the root and the latter immersed in hot water, bubbles of air will be given off from the cut surface for some little time, thus showing that the air-spaces of the root are likewise continuous with those of the stem.

The quantity of carbon dioxide evolved can be roughly determined by means of the apparatus shown in Fig. 150. The flask C containing germinating Peas kept in darkness is connected on

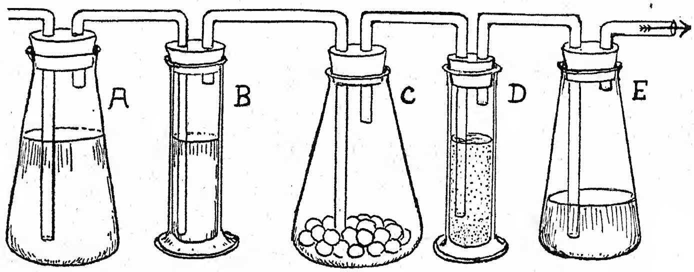


FIG. 150. Apparatus for determining the quantity of carbon dioxide produced in respiration. Description in the text. The arrow indicates the direction in which air is drawn through the apparatus.

either side with two wash bottles, and air is drawn through this system at a slow rate by means of an aspirator or a filter-pump. The first bottle (A) contains strong caustic soda to absorb carbon dioxide, while the second (B) contains lime-water to test the completeness of its removal. The air freed of carbon dioxide passes over the Peas, and the carbon dioxide liberated in their respiration is drawn into the third bottle (D) containing lime-water, where it is precipitated as the carbonate. The lime-water in the fourth bottle (E) should remain clear to ensure that complete absorption has taken place in D. By weighing the bottle D and its contents both before and after the experiment the quantity of carbon dioxide evolved can be approximately calculated.

For more accurate results it is advisable to pass the air derived from the flask containing the respiring material over calcium chloride to remove moisture, including that of respiration. Also to facilitate accurate weighing the jars D and E can be replaced by potash bulbs furnished with stopcocks; these are also weighed before and after the experiment.

The ratio between the carbon dioxide given out and the oxygen taken in is spoken of as the *respiratory quotient*, and in carbohydrate

respiration normally approximates to unity. During the germination of seeds containing a high proportion of fats, however, where substances containing a lower proportion of oxygen are involved, their oxidation to sugars during the early stages of germination results in a greater oxygen-consumption and consequently the respiratory quotient is appreciably less than unity. Conversely, when fats are being formed from carbohydrates (cf. p. 79), the respiratory quotient markedly exceeds one. Other instances of an unusual respiratory quotient are afforded by succulent plants and by ripening fruits.

Since oxygen is essential for normal respiration, its absence usually leads to a cessation of most vital processes. The stoppage of growth is most easily recognised in the failure of seeds to germinate in the absence of oxygen (p. 9). The plant, however, unlike most animals, is not immediately killed by absence of oxygen. When the latter is lacking in the surrounding air, plants carry on a process known as *anaerobic respiration*, during which carbon dioxide is also evolved. To demonstrate this, we first peel the coats off a number of soaked Peas, since air may be included between the testa and the cotyledons. A small test-tube filled with mercury is inverted into a shallow dish containing the same substance, whereupon the Peas are passed under the mouth of the test-tube and allowed to float to the top of the mercury. At first they are only partly visible, but gradually they become more and more exposed till, after some hours, they lie freely in a gaseous atmosphere which has collected at the top of the test-tube. If sufficient Peas are employed and the experiment is left for about twenty-four hours, nearly the whole test-tube will become filled with gas. This can be shown to be carbon dioxide by slipping a small piece of potash under the mouth of the test-tube when, as the carbon dioxide is absorbed, the mercury rapidly rises.

The initial phases of aerobic (*i.e.* normal) and anaerobic respiration are probably similar, although the two processes diverge in their final products. Carbohydrates are probably again broken down in anaerobic respiration, but not as completely as in the normal breathing process, and furthermore complex substances (*e.g.* alcohols) are produced which, if they accumulate, tend to poison the living plant. If, before this has occurred, the plant is restored to a normal atmosphere containing oxygen, it will usually recover and resume its ordinary life-functions. Both aerobic and anaerobic respiration involve a complex chain of imperfectly known chemical reactions, in some of which enzyme-action (including that of oxidases, p. 84) is concerned. Anaerobic respiration shows considerable similarity to alcoholic fermentation (p. 340), and in

this connection it is of interest that the group of enzymes known as zymase has been demonstrated in seeds germinating under anaerobic conditions.

The respiratory process of plants, like photosynthesis (cf. p. 212) and other functions, is markedly influenced by temperature, being slight when the latter is low and steadily increasing as it rises. The effect on respiration can be studied in the following way. To a little distilled water in a test-tube one or two drops of phenol-red are added and the whole shaken up with a little tap water.[1] A single germinating Pea is then introduced. The time taken for the solution to become yellow (owing to the action of the carbon dioxide on the indicator) is a measure of the rate of respiration of the Pea. If, with the help of a water-bath, a similar experiment be carried out at a temperature about 10° C. higher, the time requisite for the colour change will be appreciably diminished. A very slow rate of breathing is exhibited by dormant structures containing little water, *e.g.* dry seeds and many Lichens and Mosses (such as grow on tree-trunks) which remain alive, even when apparently dried up.

Our consideration of respiration has shown that it entails a breaking down and loss of substance. Since under ordinary circumstances photosynthesis is so much in excess of respiration, this loss is scarcely noticeable, but if we prevent photosynthesis by placing a green plant in the dark it is easy to show a decrease of organic substance. Two sets of about five Peas (of approximately equal size) are weighed, whereupon they are separately soaked and placed to germinate, the one in the dark, the other in the light. After about a fortnight the dry weight (p. 205) of both sets of seedlings is determined and compared with the weights of the original seeds,[2] when it will be found that the seedlings grown in the dark have lost considerably, while those grown in the light have gained.

In order that plants should survive in any natural habitat it is essential that conditions should be such that the positive gain through photosynthesis should be greater than the loss due to respiration. When these two processes exactly balance, we speak of the plant as being at the *compensation point* which varies with the species concerned. Only plants in which the respiration rate is low can subsist in deep shade or in poorly illuminated dwelling-rooms, e.g. *Aspidistra*, which has an exceptionally low compensation point.

[1] The phenol-red must be introduced in so small a quantity that on blowing through a tube into a similar sample, the indicator rapidly changes its colour.

[2] It would be better to compare with the *dry weight* of the original seeds. This can be approximately estimated by determining the dry weight in percentages of the original weight for a number of Peas, and working out the dry weight of those employed in the experiment by simple proportion.

On the other hand, so-called sun-plants normally have high compensation points.

The equation on p. 236 shows that the substances produced in respiration (viz. carbon dioxide and water) are the same chemically simple ones, from which the green plant builds up carbohydrates in the course of photosynthesis. It was pointed out in dealing with the latter process that a considerable amount of energy was required to accomplish this change (p. 211), and an exactly equivalent amount is of necessity again liberated, when the carbohydrates produced are broken down in the course of respiration. The setting free of energy during this process is manifest in many actively growing structures which often respire with such vigour that a portion of the energy liberated takes the form of heat.

A thermos flask is filled with germinating Peas or young flower-heads of the Dandelion, which are packed round the bulb of a thermometer. A bent glass tube of which the shorter arm passes to the bottom of the flask serves as a siphon to remove the accumulating carbon dioxide which would exert a harmful effect. The thermometer in this flask will soon record a higher temperature than one in a control in which cotton-wool or killed Peas to which an antiseptic has been added are substituted for the living plant-material.

The energy liberated in respiration furnishes the driving power for the plant's machinery, supporting not only life itself, but all the vital functions as well, and we can therefore understand why the latter usually cease when normal respiration is arrested. In anaerobic respiration a much smaller amount of energy (26 calories as compared with 674 calories in aerobic) is liberated, and few or no vital processes are manifested.

CHAPTER XXII

THE PHYSIOLOGY OF GROWTH

ONE way in which the energy of respiration is employed is in the process of growth, during which part of the food-material produced in the course of nutrition is used in building up new tissues. All growth comprises three distinct phases, viz. (i) the formation of new units by the division of the cells of the meristems (cf. pp. 6 and 53), (ii) the enlargement of the new cells (pp. 59, 99), and (iii) their differentiation to perform the various functions which they fulfil in the life of the plant. Of these the second is the only phase of growth visible externally and constitutes what is known as growth in popular parlance.

The restriction of growth to definite regions is a marked feature of contrast between the growth of plants and of higher animals. A further distinction is seen in the continual formation of new organs

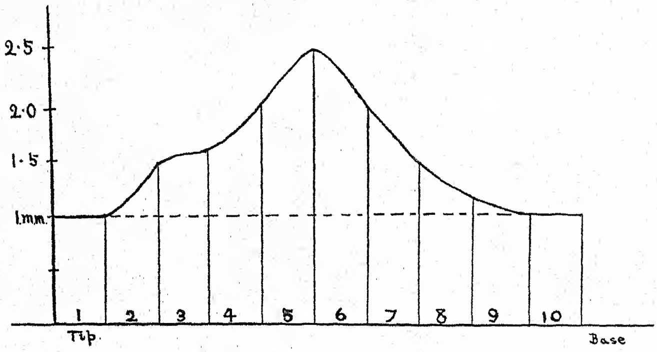


FIG. 151. Curve illustrating grand period of growth, constructed from radicle shown in Fig. 55, B. The tip and base of the radicle are indicated.

(leaves, branches, roots) from the meristems of plants, whereas in most animals the number of organs remains constant after the embryo-stage is over.

In roots elongation is restricted to a very short portion (p. 99),

whilst in stems it is spread over a much greater length. If we adopt means to compare the rate of increase of different parts of the elongating zone we shall find that it is not uniform. This can be established for roots by repeating the experiment described on p. 98 (Fig. 55) and noting the exact amount of growth in length between each pair of marks. The intervals near the tip of the root will have elongated little, but, as we pass progressively farther from the apex, the intervals become wider and wider until they reach a maximum; beyond this they again exhibit a gradual decrease up to the mature zone, where no growth in length has taken place (see Fig. 55, B, p. 99).

The result of this experiment can be more easily realised if a graph be constructed (Fig. 151) in which the abscissæ represent successive intervals, while the ordinates represent their respective lengths. The curve obtained by joining the ordinates rises to a summit and then again falls.

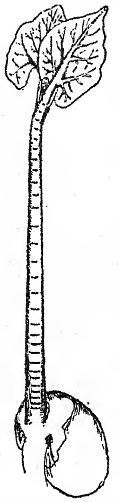


FIG. 152. Experiment to demonstrate region of growth in plumule of Runner Bean (about two-thirds natural size). At the beginning of the experiment the marks were all at equal distances from one another.

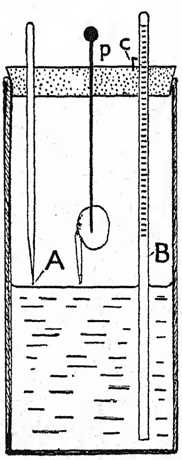


FIG. 153. Root-auxanometer (after Neilson Jones). For description, see text.

As we pass away from the tip of the root we come to older and older segments (*i.e.* intervals between two marks), and in the above experiment therefore we are comparing the amount of elongation in segments of different ages. This shows us that the cells of the newly formed segments elongate but slightly at first, but, as they get older, grow in length more rapidly until when they approach maturity their rate of elongation again decreases. This gradual rise and fall in the rate of elongation is spoken of as the *grand period of growth* and, since the cells in a given transverse plane exhibit the same rate of increase, the successively older segments epitomise the changes of the individual units.

A similar grand period is exhibited by growing stems of seedlings. If we mark the plumule of a Runner Bean in the way previously described for the root (p. 98 and Appendix XI), but over its whole length, we shall find after a day or two that the intervals have elongated over a much wider zone than in the experi-

ment with the radicle; they show, however, the same gradual increase and decrease as we pass backwards from the tip (Fig. 152). It is instructive to mark the radicle of the same seedlings for the sake of comparison.

In developing shoots the nodes usually cease to grow soon after they are formed, the later elongation being restricted to the internodes, so that growth in length takes place in a number of separate regions, *i.e.* it becomes segmented. The ultimate length of the internodes is generally not equal, those near the base and the top of each season's growth being relatively short, whilst the intervening ones often show a progressive increase in length towards the middle. This is well seen in many herbaceous plants (*e.g.* Bedstraws, Woodruff), as well as in the shoots of many trees and shrubs (*e.g.* Apple, Poplar); the following are given as examples:—

LENGTHS OF SUCCESSIVE INTERNODES (IN MILLIMETRES) ALONG A ONE-YEAR'S SHOOT

Apple .	1	2½	3	7	12	20	30	30	30	40	25	20	21	10	8	5	3
Laurel .	4	7	16	16	18	21	20	13	3	...	...	...	...	...	...	...	...

Similarly, in some rhizomes (*e.g.* Solomon's Seal, *Iris*) an analogous rhythm is exhibited, which manifests itself mainly in a variation in the diameter of the internodes.

The simplest method of measuring the rate of growth of an entire organ is, of course, direct measurement, the observations being made at regular intervals. This is most easily applicable to roots which for this purpose are grown behind glass in the box described on p. 106. To magnify the growth of a root we use a glass jar fitted with a cork (Fig. 153) through which pass two glass rods, both of which can move freely through the cork; the one (A) tapers at its lower end, while the other (B) is square-ended and graduated. A germinating Bean is fixed to the end of a long pin (*p*) which is thrust through the cork until the tip of the radicle nearly touches the surface of the water in the jar. The rod B is then pushed downwards till the water-surface makes contact with the root-tip and the position of the water-surface read on the graduated scale. A is then adjusted so that its point also touches the water-surface. As the root grows it penetrates the water.

After some time the water-level is adjusted to the new position of the root-tip by raising the rod B. In this way repeated readings on the graduated scale of B can be made with reference to the index *c*. The level of the tip of A serves as a standard of reference. The amount of magnification given by these readings is determined by the ratio between the cross-sections of the rod B and of the jar.

To magnify the growth of a shoot we use an instrument known as a *growth-lever* (Fig. 154). It is composed of a light wooden lever (*l*), with two unequal arms, working on a metal pivot (*p*) (see the small inset in Fig. 154). A small strip of lead *w* is wrapped round the short arm of the lever, so as nearly to balance the weight of the long one. The pointed end of the lever works over a

graduated arc, the divisions of which show the actual amount of movement of the short arm (Appendix XV). The growing tip of the plant is surrounded

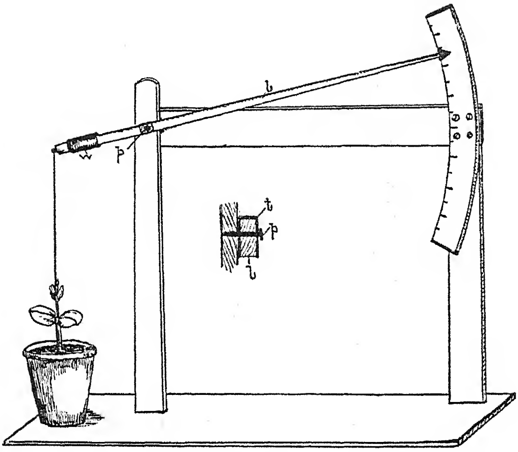


FIG. 154. Simple form of growth-lever. For description, see text. The small figure in the middle explains the mode of attachment of the lever to the upright support.

with a small pad of cotton-wool, round which one end of a thread is then firmly tied, the other end being attached to the short arm of the lever in such a way

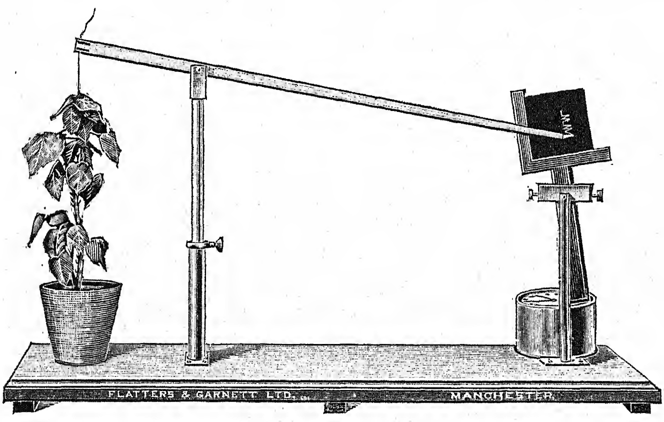


FIG. 155. Simple form of auxanometer. Description in text.

that the pointer is at the top of the scale. As the plant grows the pointer will sink and thus the amount of elongation can be noted.

It is sometimes convenient to measure the hourly growth of a plant, and for this purpose we require an instrument known as an *auxanometer*. The type shown in Fig. 155 consists of a growth-lever, the long arm of which is pointed

and just touches the blackened surface of a glass plate. The latter is held in a frame capable of movement in the plane of the lever. This movement is effected by hourly contact with the minute-hand of a clock whose position is such that the minute-hand after pushing aside the arm some little way ultimately loses contact with it, so that it swings back to its original position; this takes place automatically, owing to the glass plate being placed slightly to one side at the top of the arm.

To prepare the instrument for use, the glass plate is removed from its frame and covered with a uniform layer of soot by holding it over the smoky flame of burning camphor. The tip of the plant is attached as before to the short arm of the lever. Growth of the plant leads to a gradual fall of the pointer which consequently traces out a downward line on the sooted surface. Every hour, however, the glass undergoes a lateral movement, whereby the pointer is caused to make a horizontal mark, so that if the experiment be continued for some time we get a series of horizontal lines, the intervals between them representing the magnified hourly growths.

Both the growth-lever and the auxanometer will enable us to determine the conditions influencing growth. Thus both serve to establish that elongation is more rapid at night than during the day (provided the temperature remains approximately uniform). The marks made by the auxanometer will be farthest apart after midnight and nearest together after midday, whilst in between a perfect gradation connects the two extremes. There is thus a *daily period* in the growth of the plant, due to the alternation of light and darkness.

The increased rate of elongation in the dark is well seen in certain plants (*e.g.* seedlings, sprouting Potato-tubers, etc.), when grown in the total absence of light. Under these conditions, apart from the non-development of chlorophyll (cf. p. 8), they exhibit an exceptional elongation of the internodes (cf. p. 253), whilst the leaves remain of small dimensions (Fig. 156, A); such plants are said to be *etiolated*. Even dull light has a similar effect and many herbaceous forms (*e.g.* Willow-herbs) exhibit longer internodes in the shade of a woodland than when growing in the open. Similarly the herbs are often appreciably taller on the shady than on the sunny side of a hedge. This acceleration of growth in darkness is of great advantage in nature, especially in shoots which commence their development underground (*e.g.* plumules and shoots of herbaceous perennials), since by virtue of this feature they reach the surface rapidly.

In plants whose leaves arise from underground stems the absence of light induces exceptional elongation of the petioles, a fact which is made use of in the commercial production of Celery, Rhubarb, and Sea Kale (*Crambe*). A further interesting effect of absence of light can be observed in certain rosette-plants (*e.g.* House-leeks) in which well-marked internodes are produced under these circumstances, so that the plant acquires quite a different habit.

Apart from its influence on the rate of growth, the intensity of the light also affects the development of plant-organs. For the formation of flower-buds a higher light-intensity is normally necessary than for mere vegetative growth, though some plants can develop a specialised type of flower in weak light (cf. p. 465). Most of the vegetative buds within the crown of trees which cast a deep shade fail to develop, whereas at the margin the majority of them give rise to branches; and we may even find that the crown is denser on the south than on the north aspect.

If the leaves of two plants of the same kind growing respectively in the sun and in the shade (*e.g.* Dog's Mercury, Enchanter's Nightshade) be compared, it will be found that the blades of the sun-form are smaller and thicker than those of the shade-form (Fig. 365). A similar difference will be found between the exposed and shaded leaves of the same plant (*e.g.* the Beech). There are also anatomical differences (see p. 522).

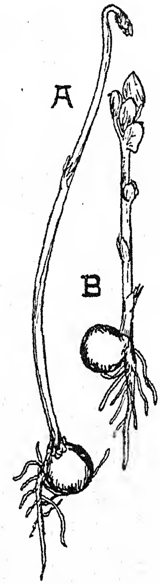


FIG. 156. Seedlings of the Pea (about three-quarters natural size), normal (B) and etiolated (A). Both are of the same age.

It is not, however, intensity of light alone that affects the manner of growth, but also its daily incidence. For instance, the so-called short-day plants, mostly natives of low latitudes (e.g. *Cosmos*), will only produce flowers if the length of daily illumination does not exceed twelve hours, whereas long-day plants, mostly natives of northern latitudes (e.g. *Rudbeckia*), are apt not to flower until the daily period of illumination exceeds twelve hours appreciably. Still other species are, however, apparently unaffected by the daily dose of light. The general phenomena of response to periodic illumination are referred to as *photoperiodism*.

It has been noted that, in order to observe the accelerating influence of darkness, it is necessary to keep the temperature approximately constant. This is due to the fact that heat and cold exert a profound effect on growth, as on other functions (cf. pp. 212 and 240), inasmuch as plants grow slowly at low temperatures, whilst with increase the rate of elongation augments until a degree of heat is attained which is injurious. Since the temperature at night is usually lower than in the day, the tendency to more rapid growth at night is masked in nature.

The effects of temperature-conditions upon growth are well illustrated by several observations on plants in their natural environment. Thus, whereas some exhibit vigorous growth already in the early spring (*e.g.* Dog's Mercury, Elm), others have to await a higher temperature and do not become active till the end of April or May (Ash, Beech, Horse Chestnut). The northward and southward extension of plants of warmer regions, again, is in part limited by the lowest temperature at which they can grow; thus certain Palms can exist in the open in the south of England, but not farther north, and many tropical plants can be cultivated in a hothouse. But such limitation is complicated by the fact that a higher temperature and illumination are necessary for seed-production than for vegetative growth. The time of flowering is markedly affected by changes of temperature. Indeed, many plants (*e.g.* Lily of the Valley) can be induced to grow and flower out of season by exposing them to cool conditions followed by heat (*i.e.* forcing them).

Apart from illumination and temperature, the most important condition influencing growth is the supply of oxygen (see p. 239). An adequate supply of moisture and nutritive material is also essential. It should be noted that modification of the external conditions in a variety of ways (even including injury) may profoundly affect the mode of growth and seasonal development of the plant as a whole or of its separate organs. By such means the growth of crop-plants can be accelerated.

The rate of elongation (phase ii, p. 242) of most plant-organs is so slow that it is necessary to employ means to magnify it; and to this general statement there are but few exceptions. The filaments of the stamens (cf. p. 5) of Grasses remain quite short until the pollen is ripe, but then a very rapid elongation takes place, amounting, in the Wheat, to nearly 2 mm. per minute. The shoots of some tropical Bamboos exhibit a similar, though somewhat less rapid, enlargement. The size attained by different plants, although variable, is nevertheless approximately constant within certain wide limits. On the one hand, we have very minute forms (*e.g.* Duckweed, Whitlow-grass); on the other, tall-growing trees and, amongst annuals, such types as the Sunflower.

The growing apex of a shoot does not move upwards in a straight line, but describes a slightly irregular course, somewhat spiral in its general character. This *circumnutation*, which is exhibited by stems and roots alike, is, however, generally not apparent unless we magnify it as by the apparatus shown in Fig. 157. This consists of a sheet of glass held horizontally, the plant whose growth is to be observed being placed underneath it and the

successive positions of the apex marked from above by affixing pointed strips of gummed paper to the glass (see Fig. 157). A small rod *a* is fixed to one of the four supports, so that its tip is situated in alignment with the mature stem and about an inch from the growing apex. Each strip of gummed paper is always so affixed that its point forms a straight line with the tip of the rod *a* and the apex of the plant, a certain, though inconstant, magnification of the movement being thereby obtained.

Good material for observing circumnutation is furnished by the plumule of the Runner Bean (before its tip bends into a horizontal position), as well as by any uncurved tendril. This phenomenon is due to more rapid growth on one side of the apex, this zone continually shifting its position round the circumference. As a result the growing tip is not straight, but exhibits a slight, often scarcely recognisable curvature, in one direction or another.

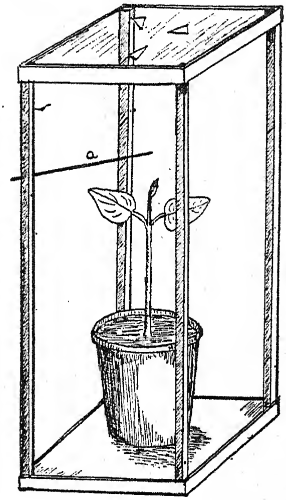


FIG. 157. Apparatus for the demonstration of circumnutation (see text).

In plants the growth of one organ is often materially influenced by that of another, so that if the one is favoured or arrested, the other exhibits a reduction or promotion. We have already met with several instances of such *correlation.* Thus in certain etiolated plants the poor development of the leaves and the arrest of the lateral buds (p. 246) is associated with greater growth of the stem. If the terminal bud is removed from a normal shoot, laterals which would otherwise remain dormant begin to sprout (cf. p. 119); spur-shoots often elongate, when the apex of the main shoot is cut off. Similarly, after removing the tip of the tap-root in a Bean or Pea, one or more of the laterals bend downwards and take its place. In those forms, moreover, in which extensive vegetative propagation obtains, reproduction by seeds is generally rare, a correlation shown by many cultivated bulbous plants. There is evidence that soluble substances (hormones) produced in the various organs of the plant may stimulate or retard the development of adjacent organs.

Pruning causes an artificial restriction of the shoot-system and aims sometimes merely at modifying the shape or size of a shrub or tree. More often its purpose is to encourage certain parts of the

branch-system. Thus the common practice of pruning fruit-trees to the outside buds aims at minimising mutual shading, and its success depends upon visualising the future development of the shoot-system. Hard pruning may lead to undue vegetative growth, but continuous pruning (*i.e.* in summer, as well as in winter) is

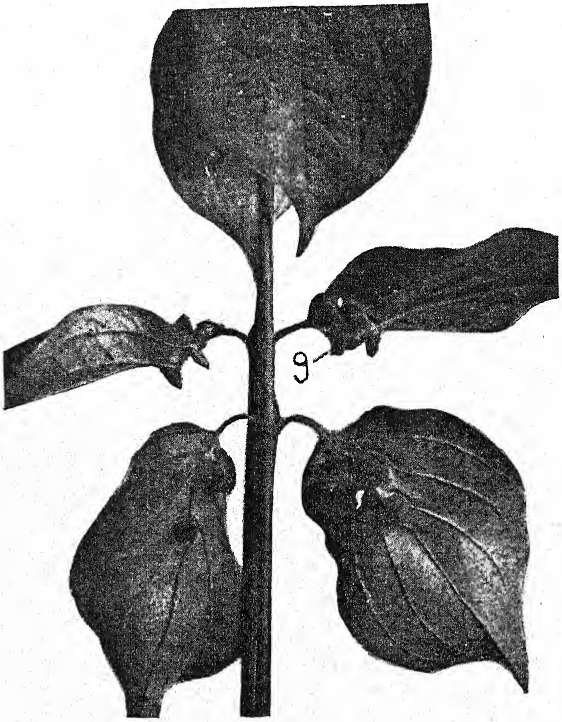


FIG. 158. Photograph of galls (*g.*) on leaves of Dogwood (*Cornus sanguinea*). [Photo. E. J. S.]

often adopted as a means of restricting food-supply to the fruiting spurs. By this means the crop of flowers, as in Roses, or fruits can be diminished, and a few large specimens in place of many small ones are obtained.

The effect of an injury to any woody axis is to cause the living cells, and especially those of the exposed cambium, to give rise to a large-celled, thin-walled tissue which at first forms a ring-shaped swelling, but often gradually becomes broader till the whole wounded surface is completely covered, the outermost cells usually becoming suberised. The tissue thus formed is called a *callus*,

and may subsequently produce adventitious shoots (*e.g.* pollarded trees) or adventitious roots as in cuttings (p. 108). Regions of injury in the parenchymatous tissues (*e.g.* of cortex or leaf) are commonly isolated from the healthy surrounding tissue by the formation of cork from a cambium produced by tangential divisions in the uninjured cells nearest the wound. In this way the attack of a parasitic Fungus is often localised.

A different stimulation to growth (hypertrophy) is sometimes consequent upon injury due to Insects or Fungus-pests which leads to the formation of so-called *galls* (Fig. 158, *g*). In Insect-galls the special growth results from the laying of an egg or eggs by the female beneath the epidermis and, in the same species of plant, different kinds of galls may be produced by different insects (*e.g.* Oak-apple gall, Cushion-gall, Fig. 159, C, Button-gall, Fig. 159, B, Bullet-gall, etc., all on the Oak). The abnormal growth known as the Witch's Broom is due to various fungal pests which lead to an exceptional branching of the attacked part, examples being commonly seen on the Cherry and Birch.

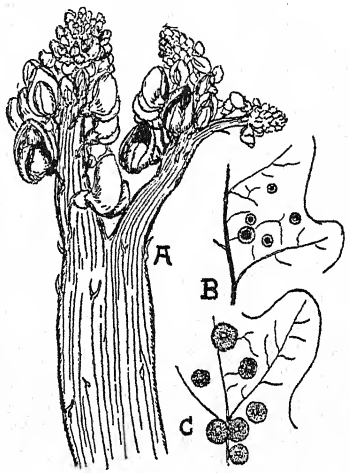


FIG. 159. A, Fasciation of the Runner Bean inflorescence. B, Button-gall of Oak. C, Cushion-gall of Oak. (All figures about two-thirds natural size.)

Little or no tissue differentiation exists in galls caused by Fungi (*e.g.* Finger and Toe disease, Fig. 217), and externally they commonly present an irregular and very variable form. Many animal galls offer a striking contrast in these respects, not only exhibiting a definite external structure (cf. Fig. 158), but, as in many of those produced by gall-flies, a complex internal differentiation due to enlargement and division of the probably chemically stimulated cells. In some the central region, where the larva of the gall-insect resides, consists of nutritive tissue composed of cells with dense cytoplasm, rich in protein material, and serving for the animal's nourishment. This region may be surrounded by a layer of sclerenchyma, whilst the outermost zone consists of parenchymatous tissue. The latter is usually well supplied with intercellular spaces, contains little or no chlorophyll, and is often traversed by vascular tissue.

Occasionally plants exhibit unusual forms of growth which are

probably a result of exceptional physiological conditions. Such *monstrosities* find expression in various ways, most commonly in so-called *fasciations* which represent a combined development of the different branches of a shoot-system, so that the whole forms a flat structure (Fig. 159, A). A similar process leads to the production of the Cauliflower, a fasciation which is inherited. Double flowers seen in many cultivated plants furnish other examples of monstrosities.

Stimulation of growth as a result of wounding is made use of in the processes known as *budding* and *grafting*, which are much employed in Rose- and Fruit-culture. In budding (Fig. 160, A and B) a shield-shaped piece of the bark, extending in as far as the wood and bearing a bud (Fig. 160, A), is cut off from one plant and inserted beneath the flaps produced by making a T-shaped incision in the bark of the stock (Fig. 160, B). In grafting (Fig. 160, C–F) a portion of a twig is removed from the one plant (the *scion*) and its tapered lower end (Fig. 160, C and E) is pushed into a V-shaped slit in the wood (Fig. 160, D) or under the bark of the stock (Fig. 160, F), so that the wood and phloem of the latter are in contact with those of the scion. In both methods the cut surfaces are usually protected from infection and drying up by covering them with grafting wax. The cut surfaces of scion and stock become intimately associated owing to fusion of the intact cells, which is usually accompanied by some cell-division.

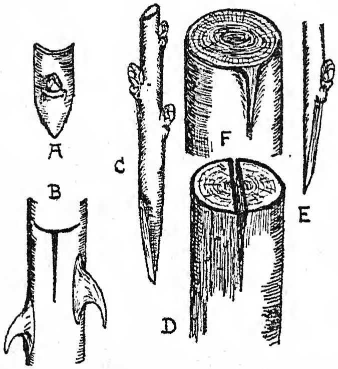


Fig. 160. Budding and grafting. A and B, Budding. *A*, bud; *B*, stock. C–F, Grafting. C–D, Cleft-grafting. E–F, Slip-grafting. *C* and *E*, scion; *D* and *F*, stock.

Grafting and budding are usually only possible between related types of plants. Those which can be associated successfully are termed *compatible*, but both compatible and incompatible strains of the same species may occur. These differences depend on such factors as relative growth-rates of stock and scion and the mechanical efficiency of the fusion. The general effect of the process of grafting in Fruit-trees is to bring about earlier and more abundant fruit-production, whilst the type of stock used may profoundly affect the ultimate size and habit of the mature tree. Grafting and budding are really special methods of pro-

pagating cuttings on another root-system and are advantageous as a means of perpetuating forms which are either infertile or do not come true from seed.

Removal of the growing tip of the stem is found to be associated with a temporary cessation of the second phase of growth, viz. enlargement. This might obviously be due to a wound-effect, but if the detached tip be immediately replaced normal growth ensues. Experiments have shown that a substance, known as a *growth-hormone*,[1] diffuses out of the growing tip which, though it has no effect on cell-division, increases the capacity of the developing cells to undergo permanent enlargement under the requisite turgor-pressure. This growth-hormone has a maximum effect in darkness and tends to check the development of the lateral buds, features which are well exemplified in etiolated plants. In the root the growth-hormone tends to retard elongation of the cells, but to facilitate their lateral extension.

One of these hormones has been identified as β-indolyl-acetic acid and, if cuttings have their lower ends immersed for a short period in a very dilute solution of this substance, the formation of roots is greatly stimulated, a fact which has been successfully employed in propagating plants of which cuttings cannot normally be rooted (*e.g.* Pear). In addition to stem-tips, hormones are also formed by growing leaves, hence the importance of using cuttings bearing young leaves. Several different types of growth-hormones are known, but they all appear to produce similar effects. They have been extracted from a wide variety of plants and are usually present in animal urine. Their movement always exhibits a definite polarity, since they only diffuse in a direction away from the growing tip.

In a tree shoot the terminal bud may alone develop or one or more lateral buds near it may develop also. These differences appear to be related to nutrition and those buds which will develop are usually already recognisable by their larger size during the winter. As soon as these begin to grow they produce growth hormones which, diffusing backwards, apparently inhibit development of the remaining buds. Similarly the growing leaves check the development of their axillary buds.

[1] For full details, see P. Boysen-Jensen, *Growth Hormones in Plants* (transl. by G. S. Avery and P. R. Burkholder). McGraw Hill Book Co., 1936 (268 pp.).

CHAPTER XXIII

THE PHYSIOLOGY OF TROPIC MOVEMENTS

As a result of elongation during growth the positions of the growing tips are continually altering, *i.e.* they exhibit a forward movement which does not take place in a straight line (p. 248). The slight curvatures occurring during circumnutation ensue from internal causes and are not due to external influences or *stimuli*. One, however, frequently meets with other growth-movements leading to curvatures which can be definitely ascribed to outside agencies. The effect of the latter is to produce a change in a receptive portion of the plant, which ultimately results in a curvature in another region, the zone of elongation. When the direction of the movement is determined by the direction of the external stimulus, we speak of the movement as a *tropic* one.[1]

Attention has been called to the influence of gravity in inducing the upright growth of the ordinary shoot (p. 15) and the downward growth of the main root (p. 106), the phenomenon being referred to as *geotropism*. The experiments already described sufficiently illustrate these general facts, and it need only be added that an organ which curves in the direction of the force of gravity is said to be *positively*, whilst one which curves the opposite way is said to be *negatively*, geotropic.

It might be thought that the downward curvature of a horizontally placed root was due to its own weight, although the negative behaviour of the shoot makes this unlikely, as well as the absence of curvature in a dead root. Even when a certain amount of resistance has to be overcome, however, roots will nevertheless be found to curve downwards when placed horizontally. This may be shown by filling a shallow vessel with mercury and fixing seedlings to corks, wedged on to the edge of the vessel in such a way that their radicles lie horizontally on the surface of the mercury. The curving roots push their way into the latter, whereas others which have been killed remain horizontal.

[1] Consult the general works on plant physiology cited on p. 193. See also C. Darwin, *The Power of Movement in Plants*. Murray, 1880 (193 pp.).

So long as the shoot and root are situated with their axes parallel to the line of action of gravity, no curvature takes place, *i.e.* there is a condition of equilibrium. As soon, however, as either occupies any position other than the vertical, this state of equilibrium is upset and curvature sooner or later takes place until gravity again acts *equally on all sides.* The condition for a geotropic curvature in an ordinary shoot or root is therefore an unequal action of gravity. If a seedling is placed horizontally in the dark and slowly rotated on its own axis, it will of course be exposed to such unequal influence; as a result of the rotation, however, all sides in succession will be subjected for an equal period of time to the stimulus and no curvature will result. In carrying out this experiment control seedlings should be supported horizontally without rotation.

FIG. 161. Klinostat. (Reproduced by permission of Messrs A. Gallenkamp & Co., Ltd.

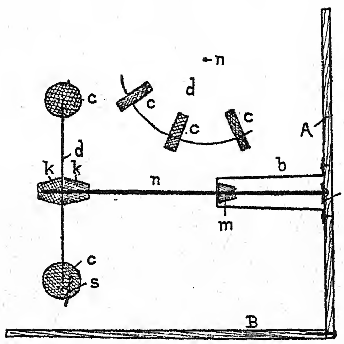


FIG. 162. Diagram to explain construction of a simple centrifugal apparatus (modified from Osterhout). For description, see text. The upper figure shows a small part of *d* from the surface.

For such purposes we use an instrument known as a *klinostat* (Fig. 161), which consists of a clock-work mechanism giving a slow and sometimes adjustable rate of rotation to a disc to which either seedlings or plants in light pots can be attached. If seedlings are employed they should be protected from drying by means of a suitable cover.

A force similar in action to gravity, and moreover one with which we can more easily experiment, is centrifugal force. When attached to the edge of a wheel, which is rapidly rotated in the vertical plane, the root of a seedling assumes a position pointing

outwards and the shoot one pointing inwards along a radius of the wheel. Thus response is precisely like that to the stimulus of gravity.

A simple centrifugal apparatus (Fig. 162) consists of a circular tin disc *d* (6 to 8 inches in diameter) to which eight flat slices (*c*, about quarter of an inch thick) of cork are fitted firmly into slightly narrower slots, cut at equal intervals (*c*, *c*) into the margin of the disc. The centre of the latter is attached with the help of two corks (*k*, *k*) to one end of a knitting-needle *n*, the other end of which is supported by a piece of tin (*b*), shaped as in the figure, and allowing free movement of the needle. The tip of the latter revolves freely in the perforated tin plate *f* and is prevented from escaping from this lower bearing by the cork *m* through which it passes. When the instrument rests on the base *B* the wheel *d* rotates in the vertical, when on *A* in the horizontal plane.

For use seedlings (*s*) with straight plumules and radicles (Appendix X) are pinned in any position to the right *or* left-hand side of each cork, all being on the same side in a given experiment. Thereupon a spray of water is directed against the *unoccupied* sides of the corks, so that the whole apparatus works like a water-wheel, the rapidity of rotation depending on the strength of the spray. If the wheel be made to revolve in the vertical plane, the result will be that the seedlings are exposed equally on all sides to the action of gravity and will consequently respond to the centrifugal force alone, assuming the position described above.

When the wheel is rotated horizontally the seedlings are exposed to the one-sided influence, both of gravity and centrifugal force, and will be found to take up a position with the radicles pointing outwards and downwards, and the plumules inwards and upwards; as the rapidity of rotation is increased, both radicles and plumules become more nearly horizontal. The ultimate position of the two parts of the seedling is a resultant of the combined action of the horizontal centrifugal force and of the vertical force of gravity. Thus they come to lie at an angle which represents the position of equilibrium between these two forces. Such experiments show that centrifugal force and gravity can have a combined effect upon the plant.

There are organs, such as creeping shoots and rhizomes, which respond neither positively nor negatively to gravity, but are in a position of equilibrium when more or less at right angles to its line of action, and such structures are said to be *diageotropic*. If a rhizome is planted in an inclined position the growing zone curves until the apex again lies horizontally. The lateral roots and the horizontal branches of trees also have a different position of equilibrium to that of the erect axes. If the lateral roots of the first order are shifted from their customary position, the growing parts curve until they form the same angle with the horizontal as before (p. 106). The position occupied by laterals probably depends on some influence of the main axis, since removal of the

latter causes one or more of the laterals to grow vertically (cf. p. 249).

A given organ does not always show the same response to gravity in all stages of its development. Thus, in the Poppy (Fig. 163) the upper part of the flower stalk is positively geotropic before the flower opens (*a*), diageotropic during the process of opening (*b*), and negatively geotropic when fruit-formation begins (*c* and *d*). Similarly, many rhizomes (*e.g.* the Solomon's Seal) are diageotropic, but their tips become negatively geotropic prior to the formation of the overground shoots.

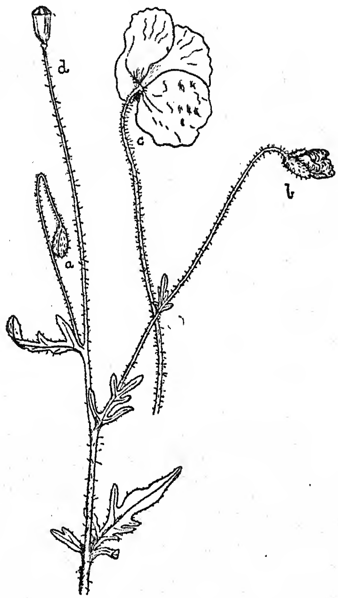


FIG. 163. Flower-buds, flowers, and fruit of *Papaver*, showing the successive positions (*a–d*) of the flower-stalk in successive stages of development (about one-third natural size).

If a seedling, in which plumule and radicle have been marked in the way described on p. 98, is placed horizontally in a dark box (cf. p. 106), it will be found that the curvature after twenty-four hours has in both regions taken place approximately in the zone of maximum elongation (Fig. 164). Moreover, it will be noticed that both the extreme tip and the older part of each organ have remained almost straight. Various experiments suggest that geotropic stimulation is primarily received by the apical region of the root.[1]

The growth-hormone (p. 253) produced by the root-tip normally diffuses evenly backwards, causing an equal retardation in the rate of elongation. When, however, the root is placed horizontally, the hormone diffuses mainly along the lower side, so that the upper elongates more rapidly than the lower leading to a downward curvature. If the tip of a stimulated root be removed and replaced with an intervening layer of gelatine, the behaviour is similar to that of an uninjured root. If the tip of an unstimulated root is removed and replaced on the stump towards one side, a subsequent curvature in a direction towards the side bearing the tip is observed;

[1] In the root-tip and in the starch-sheath of some plants there occur large, readily movable starch-grains which have been thought by some botanists to be associated with graviperception, but their rôle is altogether obscure.

this is due to the retarding hormone diffusing in towards the side which becomes concave. A block of gelatine or agar-agar, which has been in contact for some time with a root-tip, can be substituted for the latter. This demonstrates that the living apex is only essential as a producer of the hormone, but that when this has diffused into a suitable medium, such as a small cube of gelatine, the latter can serve in place of a root-tip.

Similar experiments can be performed with shoot-apices, but since the hormone here accelerates elongation, a negative curvature

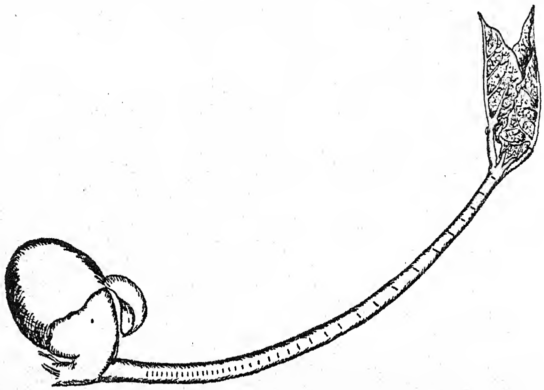


FIG. 164. Experiment to demonstrate region of geotropic curvature in the plumule of a Runner Bean placed horizontally.

is produced when the stem is placed horizontally. Tips of growing leaves behave similarly to stem-tips, and the coleoptile (p. 32) of Grass seedlings is particularly suitable for these experiments.

Intercalary meristems marked by a soft region either towards the base or the apex of the internode occur in Grasses, Carnations, and members of the Labiatæ (cf. p 54). They are an important means of enabling the stems to become erect if the shoot is laid prostrate by wind or rain. In fact, whereas in most plants, when the stem becomes horizontal, the older part remains prostrate and only the actually growing part becomes erect, the whole shoot in Grasses soon assumes an upright position under these circumstances. This is due to the fact that, when horizontal, the intercalary meristems are stimulated to growth which is more active on the under than on the upper side.

The ordinary erect shoot responds to one-sided light by curving more or less markedly towards the source of illumination (p. 14, Fig. 6, B), so that it exhibits *positive phototropism*. Aerial roots (*e.g.* Ivy, Fig. 61) and the tendrils of the Virginia Creeper and

Vine furnish the commonest instances of *negative phototropism*; a few subterranean roots (*e.g.* Mustard) are, however, also influenced negatively by one-sided light, although the majority of roots appear to be unaffected. Careful experiments have shown that the response is largely dependent on the intensity and duration of the illumination.

For exact experiments on phototropism it is best to employ a dark chamber of the type shown in Fig. 165. This is made light-tight and painted black inside to prevent reflection. A small slit is situated at one end of the box, while the opposite end is hinged and serves as a door for introducing and removing plants.

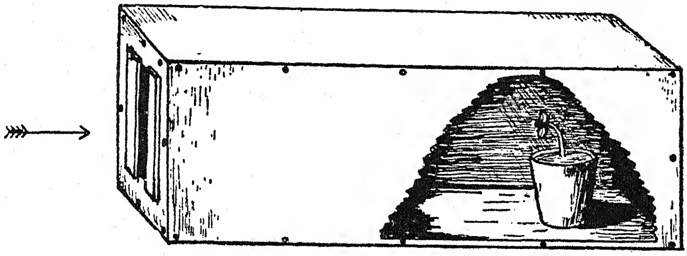


FIG. 165. Dark chamber for experiments on phototropism (see text). The arrow indicates the direction of the light.

In open spaces in nature light and gravity act together in producing the upright growth of the ordinary shoot, but at the edges of dense thickets and in hedges, where one-sided light comes into play, positive phototropism is stronger than the negative geotropism, so that the shoots grow out towards the light. With the help of the dark chamber, it can be shown that the relative effect of the two influences varies in different plants; thus the shoots of some (*e.g.* Pea) assume an almost horizontal position, whilst others curve to a less extent (*e.g.* Cress, Runner Bean), showing that they are more strongly affected by gravity.

That erect shoots do not curve, when uniformly illuminated on all sides, is shown by everyday observation, as well as by the fact that no curvature takes place when a plant is rotated on a klinostat at right angles to the source of light, since each side is then in turn equally illuminated. If we mark the plumule of a seedling at equal intervals and then expose it to one-sided light in the dark chamber, it will be found that, as in geotropic curvatures, the bending ensues in the region of maximum elongation.

Another analogy between the two kinds of phenomena is furnished by plant-organs which respond to the influence of light by taking up a position more or less at right angles to its direction.

Such *diaphototropism* is most strikingly exhibited by ordinary dorsiventral foliage-leaves and is responsible for the definite position in relation to light, assumed by the blade during development, a feature which is specially noticeable in leaf-mosaics (cf. p 121). There are, however, leaves which are negatively geotropic and grow vertically (*e.g.* Iris).

A further similarity between phototropism and geotropism lies in the change of phototropic response exhibited by the flower-stalks of some plants. Thus, in the Ivy-leaved Toadflax (Fig. 166), very common on old walls, the flower-stalks bend towards the light (*i.e.* are positively phototropic), but during the development of the fruit they curve away from it (see right-hand figure); in this way the ripening fruits are carried in the direction of the wall, so that the seeds are often shed in its crevices.

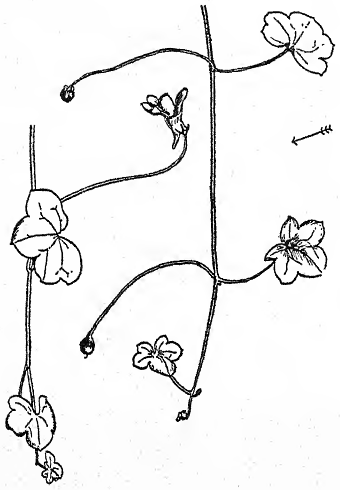


FIG. 166. Change of phototropic response in the flower-stalks of the Ivy-leaved Toadflax (*Linaria cymbalaria*). The arrow marks the direction of the light.

The power of perceiving one-sided light has also been shown to be localised in certain regions, a fact which can be demonstrated in young seedlings of Canary-grass in which the leaves of the plumule have not yet burst through the coleoptile. The tips of some are covered with small caps (Fig. 167, *c*), each about half an inch long and made by twisting silver paper round the point of a pin, whilst others (Fig. 167) are left uncovered. The whole pot is then placed in the dark chamber (Fig. 165). After about twenty-four hours the uncovered seedlings will have bent in the usual way towards the light, whilst the others have remained straight. The perceptive power is therefore here localised in the upper part of the coleoptile and, as in the geotropic curvature of roots, there is a conduction of the stimulus to the region in which bending takes place.

In phototropism, as in geotropism, diffusion of hormones is involved. As we have already seen (p. 253) the effect of the growth-hormone in stimulating elongation is reduced by light, but in addition the unilateral illumination causes a diminution in the rate of diffusion on the illuminated side. Thus the shaded side

of a shoot receives more hormone, which is also more effective, so that greater growth ensues here and the shoot curves towards the light. With Grass seedlings experiments on phototropism, involving the removal of the tip of the coleoptile, can be performed as with geotropism.

An unequal distribution of moisture has been shown to produce a positive growth-curvature in roots (p. 107), a phenomenon known as *positive hydrotropism*. This phenomenon can also be demonstrated by the following method (Fig. 168). A small wire sieve is

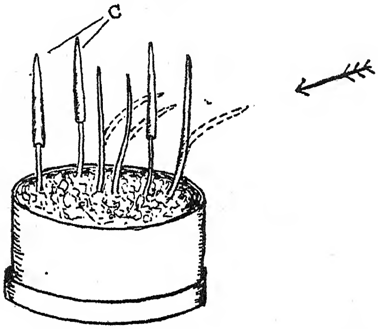


FIG. 167. Experiment to demonstrate the localisation of light-perception in young seedlings of the Canary-grass (*Phalaris*). The arrow shows the direction of the incident light. *c*, caps of silver paper. The positions occupied by the uncovered seedlings at the end of the experiment are indicated by dotted lines.

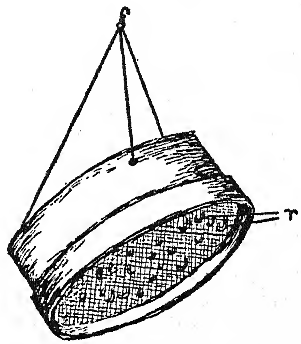


FIG. 168. Experiment to demonstrate hydrotropism in roots (see text). *r*, the curved radicles.

filled to the depth of about half an inch with damp sawdust in which Cress-seeds are sown, the whole being then covered with damp blotting-paper. After this the sieve is suspended in moderately moist air at an angle of about 45°, whilst a similar sieve is hung up horizontally. When the radicles of the Cress-seedlings emerge through the meshes of the sieve they will be found in the sloping one to curve through a right angle, so that they again reach the damp sawdust (Fig. 168, *r*). This is due to the vertically growing radicles, on entering the relatively dry air below the sieve, being nearer to the moist surface on one side than on the other, and hence the necessary conditions for a hydrotropic curvature are realised. On the other hand, in the horizontal sieve, no such curvature is observed, since all sides of the radicles are equally stimulated by the moisture.

In nature hydrotropic curvatures are chiefly shown in drier

soils by the finer branches of the root-system, where they are of considerable value in carrying these rootlets into regions of greater moisture. Negative is much rarer than positive hydrotropism and has been observed in Fungi.

There is evidently a certain parallel between the various tropic curvatures, especially between geotropism and phototropism. In both there are organs which respond positively, others which respond negatively, and still others which place themselves at right angles to the directive stimulus. Further, the curvature always ensues in the zone of elongation, somewhere about the region of maximum growth in length, and is due to the convex side elongating more rapidly than the concave. Moreover, the region of perception is probably always separated from the region of curvature and consequently conduction must occur. This has been shown in both phenomena to be due to the same growth-hormone which, under stimulation, diffuses unequally backwards.

The same stimulus may produce a totally different effect in different organs (*e.g.* gravity causes roots to curve towards the earth, shoots to curve away), so that there is obviously no definite relation between the cause of the impression and the type of effect produced. Moreover, we have seen that in certain plants a given organ responds in a different way to the same external agency in various stages of its development, as in the flower-stalks of the Poppy and the Ivy-leaved Toadflax. Such changes in response emphasise the complexity of the phenomenon and suggest that the rate of diffusion of growth hormones is part only of an elaborate mechanism.

CHAPTER XXIV

THE PHYSIOLOGY OF PLANT-MOVEMENTS
(continued)

CERTAIN plant-organs exhibit growth-curvatures which are a result of direct contact with some foreign body and thus differ materially from those discussed in the preceding chapter. The commonest examples of such curvatures are furnished by *tendrils* (cf. p. 17), whose morphological nature may first be considered.

Most such tendrils[1] are modified leaves or parts of leaves, as in many members of the Leguminosæ and *Cobæa scandens*, a common greenhouse climber. In the Leguminosæ one or more leaflets of the pinnate blade may be modified as tendrils, the consequent reduction of photosynthetic surface being often compensated by the enlargement of the stipules and the production of green wing-like expansions by the stems and petioles; all of these features are well illustrated by the Sweet-pea (Fig. 169, B). In *Lathyrus aphaca* (Fig. 74, D) the whole blade is replaced by a single tendril, the large stipules taking over the normal work of the leaf. In seedlings of this plant the lower leaves not infrequently possess small blades with relatively small stipules, the latter becoming larger in the upper leaves as the blade becomes reduced.

In *Cobæa* the ultimate segments of the compound leaves are similarly replaced by tendrils, the tips of which are provided with a claw-like hook giving a firmer grasp on the support. In a few plants (e.g. *Clematis*, Canary Creeper) the leaf-blade remains unmodified, but the petiole acts like a tendril and entwines the support.

Branch-tendrils are relatively rare; instances are the tendrils of the Vine, the Virginia Creeper (*Ampelopsis*), and the Passion-flower. In the last-named plant the simple tendrils clearly arise in the axils of the leaves, so that their branch-nature is manifest. In the Vine and Virginia Creeper (Fig. 169, A) the branched tendrils arise at

[1] A considerable number of data on climbing plants will be found in C. Darwin, *The Movements and Habits of Climbing Plants*. J. Murray, 1905 (208 pp.).

each node, on the side of the stem opposite to that bearing a leaf. This is due to the fact that each segment of the stem ends in a tendril which is bent over to one side, the growth of the main axis being continued by the axillary bud between the tendril and the leaf situated opposite to it, so that the whole stem is a sympodium (cf. p. 118).

In the White Bryony (*Bryonia*, Fig. 9, p. 16) the exact nature of the simple tendrils is doubtful; each arises together with a short branch (Fig. 9, B, *br.*), and frequently an inflorescence as well,

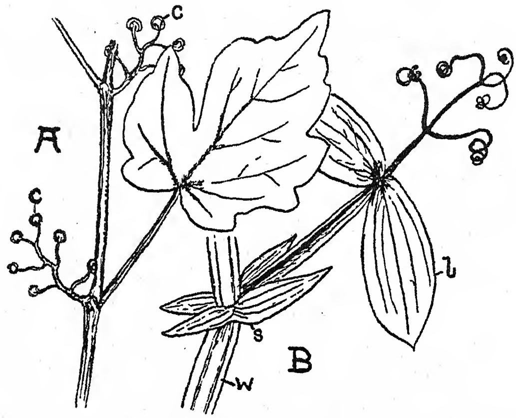


FIG. 169. Tendrils A, of the Self-climbing Virginia Creeper (*Ampelopsis Veitchii*), and B, of the Sweet-pea (*Lathyrus odoratus*) (natural size). *c*, attaching cushions; *l*, unmodified leaflets; *s*, stipule; *w*, winged stem.

from the axil of a foliage-leaf. Some regard the tendril as a modified first leaf of the short branch, whilst others look upon it as an accessory branch developed in the leaf-axil (p. 115). Such an accessory branch may represent part of an abbreviated branch-system which is precociously developed on the axillary bud and whose subtending leaf is suppressed.

The tendrils or their branches, when young, are almost straight and constitute flexible structures composed of soft turgid tissue. At this stage their growing tips exhibit a very pronounced circumnutation (cf. p. 248) which materially increases the probability of their coming into contact with a support. If this occurs, the side of the tendril opposite to that touched is stimulated to grow more rapidly, whilst that in contact with the support continues to grow at the same rate as before. This brings about a curvature of the tip of the tendril (cf. Fig. 9, A) and, as a consequence, new parts of it come into touch with the support and thus receive a fresh

stimulus; moreover, the resulting curvature is not confined to the part actually in contact, but also affects adjacent parts of the tendril. In this way more and more of the growing tip firmly grasps the support.

After this the part of the tendril between the parent-plant and the support gradually coils up into a close spiral and, since both ends of the tendril are fixed, the coils of this spiral of necessity exhibit a reversal at some point or other (Fig. 9, B). Hence an elastic spring-like connection is developed, so that the risk of the plant's being torn away by gusts of wind, etc., is diminished. Soon after its attachment the tissue of the tendril begins to thicken and lignify, so that it loses its soft flexible character. Tendrils which fail to reach a support wither away and sooner or later generally drop off. Where climbing is accomplished with the aid of sensitive petioles, the mechanism is similar, although the effect does not extend beyond the region of contact.

The effect of a contact-stimulus can be imitated by gently stroking the under surface of a White Bryony tendril with the finger for about a minute. A curvature almost immediately becomes apparent and is generally very pronounced before long. The changes leading to the curvature of a tendril depend, not upon the actual contact, but upon rubbing against some foreign body. This has been proved by placing tendrils in contact with a support and ensuring the absence of all vibration, when no curvature is observed. Tendrils, moreover, are not stimulated by contact with fluid bodies, so that the impact of rain-drops is without effect.

The negatively phototropic tendrils of the Self-climbing Virginia Creeper exhibit quite a different method of attachment. The tips of their branches swell up into little cushions (Fig. 169, A, *c*) which, on meeting a wall, cling to it by the production of an adhesive substance and then gradually flatten out to form sucker-like discs which adhere very tenaciously to the surface. In the ordinary Virginia Creeper and the Vine the tendrils mostly function in the usual way, but should their tips come into contact with a firm surface they develop similar cushions which subsequently form adhesive discs.

The mechanism for encircling the support in stem-twiners (p. 17) is totally different from that found in tendrils, since no amount of stroking of a twining stem will produce any response. It seems probable that a peculiar action of gravity here plays some part, since stem-twiners can only coil round a more or less vertical support and lose their power of twining, when rotated on a klinostat. Furthermore, if a Runner Bean for instance, which has already wound round a support, is kept in an inverted position, some of the

last-formed coils untwine and commence to wind in the opposite direction (Fig. 170).

The direction of twining is usually constant for any given kind of stem-climber, taking place either from left to right (*i.e.* clockwise, as in the Hop, Fig. 10, Honeysuckle, and Black Bindweed) or from right to left (*i.e.* counter-clockwise, as in *Convolvulus* and the Runner Bean), but the Woody Nightshade (*Solanum dulcamara*) which is an occasional climber sometimes twines in one direction and sometimes in another. Among British plants the Honeysuckle (*Lonicera*) is the only woody twiner, but in the jungles of the Tropics numerous larger forms known as lianes are common (cf. p. 185).

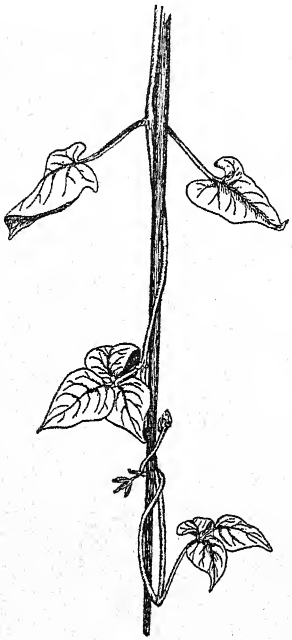


FIG. 170. Effect of inversion on the twining stem of the Runner Bean.

The curvature of the tentacles of the Sundew after an insect has been entrapped (cf. p. 221) is due to a contact stimulus, although a chemical influence may also be involved. Here we have a good example of transference of stimuli since, after the particular tentacles bearing the insect have curved inwards, other tentacles not in contact with it follow suit.

Movements due to contact-stimuli, but differing from those hitherto noticed in not depending upon unequal growth of the two sides of the curving organ, are seen in the stigma of *Mimulus glutinosus* and in the stamens of the common Barberry. In the former the stigma consists of two flat spreading lobes (Fig. 171, A, *s*.) which, on being touched (*e.g.* by the tongue of a pollinating insect, cf. p. 460), close together in the way shown in Fig. 171, B. The six stamens of the Barberry-flower project outwards, so that their anthers are some distance from the stigma, but, when the bases of the filaments are touched as by an insect, the stamens thus stimulated spring up into a vertical position, thereby covering the insect with a shower of pollen. In both of these plants the movement is due to sudden decrease of turgidity in certain cells.

Many leaves exhibit so-called *sleep-movements*. In these the petiole takes up different positions in darkness and in light, the

swollen leaf-base, or *pulvinus* (Fig. 172, *p.*), being the region of movement. Movement is facilitated by a flattening of the vascular

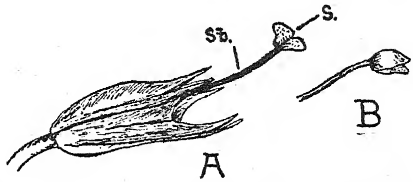


FIG. 171. Response of the stigma of *Mimulus glutinosus* to contact-stimuli. A, Normal position. B, With the two lobes of the stigma closed together, after a stimulus has been received. *s.*, stigma; *st.*, style.

tissue in a plane at right angles to the direction of curvature (Fig. 172, *Pu.*), the necessary rigidity being attained by a greater development of the cortex, which consists of large, turgid, thin-walled

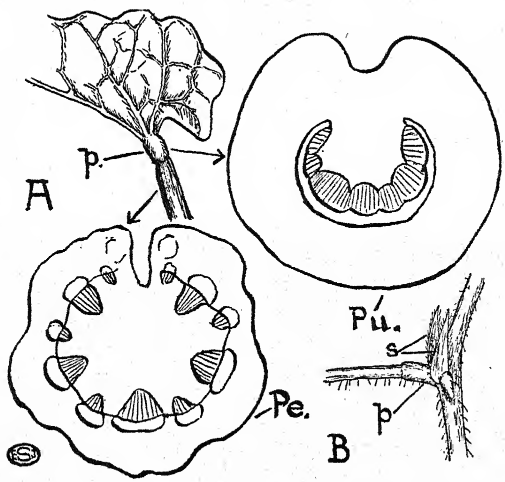


FIG. 172. A, Pulvinus of Runner Bean (*Phaseolus*) and diagrams of transverse sections of the pulvinus (*Pu.*) and the petiole (*Pe.*). B, Pulvinus of Sensitive Plant (*Mimosa pudica*). *p.*, pulvinus; *s.*, stipules.

parenchyma-cells. The fall of the leaflet at dusk is accompanied by a decrease in the turgidity of the cortical cells on the lower side of the pulvinus, whilst at the same time some of their watery sap escapes into the intercellular spaces. This is due to a change in the permeability of the protoplasm and, as a result of the infiltration of the intercellular spaces, the whole pulvinus acquires a more transparent, deeper green appearance. At dawn the cells of the

pulvinus once more become turgid and the leaf assumes the day-position.

A common example of sleep-movements is furnished by the Wood Sorrel in which the leaflets droop down at night (Fig. 173). Such movements can also be induced by the influence of contact. Thus, if the leaflets of the Wood Sorrel be repeatedly flicked with the finger, they will after some time assume the night position (Fig. 173, N). Other kinds of Wood Sorrel which are cultivated in conservatories display these changes much more rapidly. The

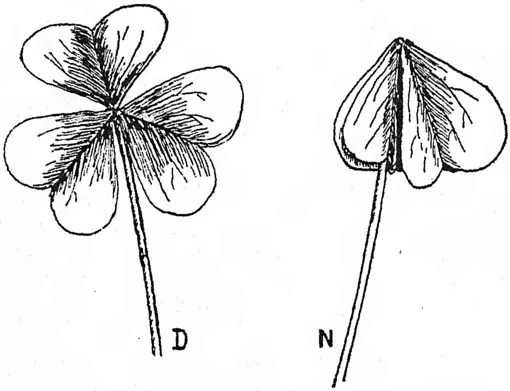


FIG. 173. Leaves of the Wood Sorrel (*Oxalis acetosella*) (natural size). D, day-position. N, night-position.

most striking instance is that of the familiar Sensitive Plant (*Mimosa pudica*), a member of the Leguminosæ. Here not only do the leaflets fold together in pairs, but with a sufficient stimulus the whole leaf performs a downward movement. Moreover, after this has happened other adjacent leaves may undergo the same change, so that here there is a rapid transference of the original stimulus. A very sudden fall in the turgidity of the pulvinus results when the leaf is touched or injured. All these organs sooner or later recover their normal position, after the effect of the stimulus has passed away. Sleep-movements are also well seen in the Dutch Clover (where the leaflets move upwards and lie face to face at night) and other members of the Leguminosæ (cf. Fig. 174). An advantage of the assumption of a more or less vertical position by the leaflets at night may be the smaller surface from which radiation can take place, so that relatively little dew is deposited. Sleep-movements of leaves are seen much more commonly in tropical plants than in our own flora.

Many flowers close at night, as for example the Tulip, the White

Water-lily, and the Wood Anemone, and these changes are analogous to the sleep-movements just discussed. Similarly, the flower-heads of many members of the Compositæ close up at certain times, most commonly on the approach of night (*e.g.* Daisy), but sometimes at midday, as in *Tragopogon*, whence the popular name for this plant "John-go-to-bed-at-noon." Night-flowering plants (*e.g.* Evening Primrose, Tobacco, cf. p. 464) have their flowers closed during the daytime, but open them at night. In the Carrot it is the whole inflorescence that hangs down at night. By means of all such floral movements stamens and stigma are protected at times when the pollinating insects are not flying.

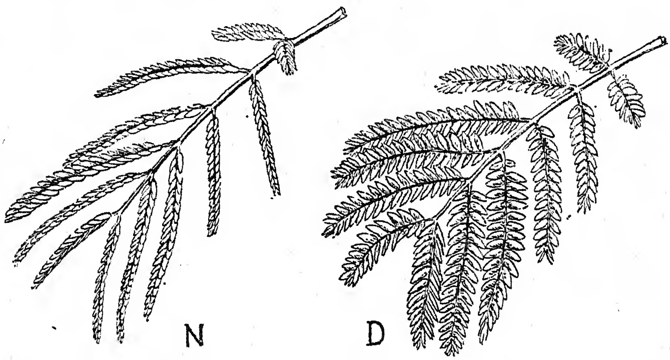


FIG. 174. Day- (D) and night- (N) positions of the leaflets of the bipinnate leaf of *Acacia lophantha* (natural size).

The external causes of sleep-movements and of these diurnal changes on the part of flowers are very complex, but since they generally follow on the daily alternation of light and darkness, associated with which is a change of temperature, these are no doubt the two stimuli especially concerned; other factors, partly rhythmic responses, are also involved, as is obvious in *Tragopogon*. That change of temperature can sometimes be a prime cause of these movements is shown by the Tulip, whose flowers open out widely in a warm room. Most movements of floral organs are accompanied by growth-changes.

In many of the movements just considered, the response exhibited is independent of the direction of the stimulus, and such are usually termed *nastic* movements. They therefore contrast with the directional response seen in tropic movements. But there are some plant-movements (*e.g.* those of certain tendrils) which cannot easily be allocated to one or other of these categories.

All the movements of plant-organs discussed in this and the

preceding chapter take place only when other external conditions are suitable, the most important of these being an adequate temperature. At low temperatures the movements are either not exhibited at all or are performed very slowly. In the absence of the necessary amount of oxygen for respiration they usually cease (cf. p. 239), and the same result is obtained if the atmosphere around the plant contains small quantities of anæsthetics (*e.g.* chloroform). Unless, however, these arresting influences operate for a considerable period, their paralysing effect is only temporary.

If an organ be exposed to a stimulus for a certain minimum time (*presentation time*), a subsequent response will occur even if the stimulus cease to act, a fact especially obvious in geotropic and phototropic phenomena. To show this, a seedling is placed horizontally for about half an hour, its lower side being marked with Indian ink, so as to be subsequently recognisable. Before any curvature of the radicle is manifest the seedling is fixed on the klinostat, so that gravity now acts equally on all sides in succession. Nevertheless, after some little time a curvature of the radicle is observed, this taking place towards the marked side. A similar result would be obtained with a plumule exposed, for the same period, to one-sided action of gravity or light, and fixed on the klinostat before a bending movement is apparent. These experiments demonstrate that a period (*reaction time*) elapses between the reception of the impression and the occurrence of the curvature (cf. p 257) and further that, when once a sufficient stimulus has been received, it cannot be obliterated by subsequent exposure to uniform conditions. Similarly, if a tendril is stroked for a short time and then left untouched, a subsequent curvature nevertheless takes place.

Weak stimulation, if sufficiently prolonged and continuous, has the same effect as a stronger stimulus of shorter duration. But the fact that a small amount of stimulation has no effect, if interrupted for an appreciable time, is an important safeguard against unnecessary response in nature. If intermittent stimuli are applied, there may be a summation of their effects, resulting in response, providing the intervals between successive stimuli are sufficiently short.

Plants, in common with animals, thus possess a certain power of movement, though of a more limited character. All growing organs are able to bend and thus to adjust their position in relation to external influences, and such movements may be exhibited even by mature organs. Amongst the green Algæ there are some that swim about freely. Many ripe fruits (cf. Chapter XXXVIII) and other structures show movements of another kind, which depend on differences in the amount of shrinkage or expansion of dead cells.

CHAPTER XXV

SIMPLE PLANTS

PLANTS exhibit a great variety of external form, but nevertheless can be assembled in groups having many features, both of structure and life-history, in common. Very many vegetable organisms are, however, far simpler in every way than the highly complex Flowering Plant. For example, whole groups of lower plants lack true roots and possess no vascular system. A specialised conducting tissue consisting of xylem and phloem is only encountered in the Flowering Plants (Angiosperms), in the Gymnosperms (*e.g.* Conifers), and in the Ferns and their allies (Horsetails, Clubmosses, etc.), whilst it is lacking in Mosses, Liverworts, Fungi, and Seaweeds.

The Vegetable Kingdom can therefore be conveniently divided into vascular and non-vascular plants.[1] This difference may perhaps be related to the fact that a considerable percentage of the latter flourish in wet or damp habitats, for it is only amongst some of the larger and definitely terrestrial Mosses that anything simulating the vascular tissues of higher plants is developed. Many non-vascular plants possess a type of body called a *thallus* which exhibits no definite stem and leaves, and is often a mere flattened cellular expansion (Figs. 187, 188). The further classification of the Vegetable Kingdom (cf. p. 603) is based mainly on the methods of reproduction and the structure of the reproductive organs.

A considerable number of the simplest types of plants are unicellular, and such minute organisms, by their abundance, often cause the green colouration of small stagnant pools. Some of the plants commonly responsible for this phenomenon belong to the genus *Chlamydomonas*, one of the most striking characteristics of which is the power of movement from place to place, usually associated with animals.

Each individual consists of a spherical or oval cell, about one-fiftieth of a millimetre in diameter. The cell is bounded by a thin

[1] Since many so-called vascular plants possess no true vessels, these terms are apt to be misleading, but long use justifies their retention.

wall which is often produced into a slight colourless papilla at the front end (Fig. 175, A, *h*), *i.e.* that which is foremost during movement. There is usually a single large *chloroplast* (*c*), having the shape of a deep cup with a very thick base and with the opening directed forwards. Within the thickened part is embedded

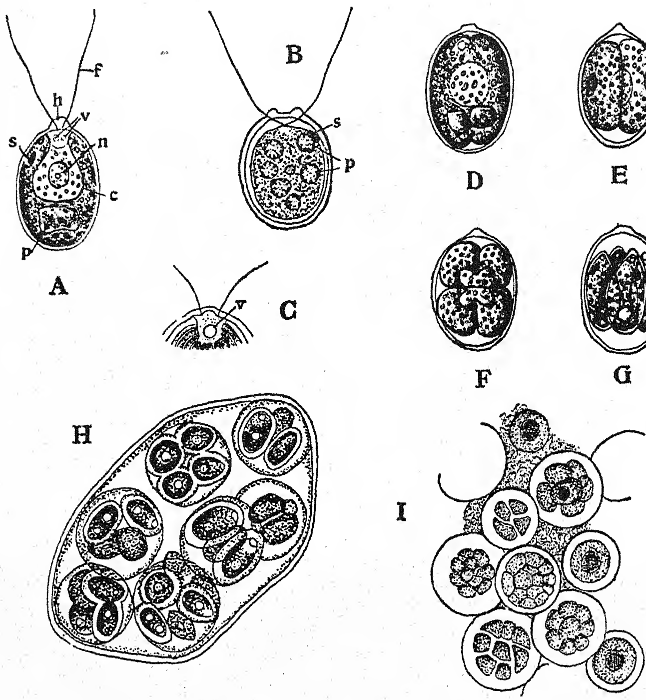


FIG. 175. Structure of individuals and asexual reproduction of *Chlamydomonas*. A, Individual of *C. angulosa*. B, ditto of *C. sphagnicola*. C, front end of a cell greatly magnified. D–G, stages in the asexual propagation of *C. angulosa*. H, I, *Palmelloid* stages of two different species. *c*, chloroplast; *f*, flagellum; *h*, anterior papilla; *n*, nucleus; *p*, pyrenoid; *s*, eye-spot; *v*, contractile vacuole. (A, D–G, after Dill; B and I, after Fritsch; H, after Goroschankin.)

a *pyrenoid* (cf. p. 43), surrounded by a sheath of small starch-grains (Fig. 175, A, *p*), but after active photosynthesis starch may also be found stored in other parts of the chloroplast. Adjacent to the rim of the latter lies a small red speck or streak of modified cytoplasm known as the *eye-spot* (*stigma*) (Fig. 175, A, B, *s*), which is concerned with the perception of light intensity (cf. below). A single nucleus (*n*) lies in front of the pyrenoid suspended by cytoplasmic strands within the cavity of the chloroplast.

If a stationary individual be observed under the high power of the microscope, a pair of small highly refractive vacuoles will be recognised in the clear cytoplasm at the front end (Fig. 175, A, C, *v*); when these are watched closely they will be seen, alternately, to enlarge gradually and then suddenly to collapse. Similar *contractile vacuoles* occur in many unicellular plants, as well as among the lower animals, and they probably serve to get rid of excess water and waste products.

The movement of the *Chlamydomonas*-individuals is accomplished by means of two delicate thread-like outgrowths, the *flagella* (Fig. 175, A, *f*), which lie in a plane at right angles to that of the two contractile vacuoles (Fig. 175, C) and arise close together from the front end. They are more readily seen after adding a drop of iodine, which has the effect of killing the organisms without much change, and not only brings out the flagella, but also makes the nucleus more distinct. The flagella are whip-like prolongations of the cytoplasm which, by their rapid backward strokes, pull the plant through the water, the movement being accompanied by a rapid rotation of the organism upon its axis. In returning to the front position, the flagella are not stretched out, and thus do not counteract the effect of the back stroke, the movements being thus comparable to those of the arms in swimming. The rate of travel of these organisms is rapid relative to their size. Thus, a *Chlamydomonas* occupies a mere fraction of a second in traversing a distance equal to its own length, whilst for a liner this evolution requires several seconds.

The direction of movement is influenced by various external stimuli, such as light, distribution of chemical substances, etc. If some water containing *Chlamydomonas* be placed in a glass bottle covered, except for a small aperture on one side, with black paper, after exposure to illumination for some hours, the organisms will be found to concentrate in a dense cluster at the spot where the beam of light penetrates. If, however, the latter is very intense, the plants swim away from the illuminated region. The influence of the direction and intensity of the light on such movements is spoken of as *phototaxis*. This is an example of so-called *tactic movements* in which the whole organism moves from place to place in a direction determined by an external stimulus. Like the movements of the cytoplasm within the cells of higher plants (cf. p. 40), the movement of these unicellular organisms can be temporarily arrested by slight traces of anæsthetics.

Chlamydomonas, with the help of its chloroplast, is able to manufacture food from simple inorganic substances like any other green plant, and consequently the cell grows. After attaining a

certain size it comes to rest, draws in its flagella, and begins to form *daughter-individuals* (Fig. 175, D–G). The protoplast contracts slightly away from the wall and, after nuclear division has taken place, gradually constricts into two equal portions (E), each containing half the nucleus, chloroplast, etc. The resulting segments may divide again (F, G), and these even for a third time, the successive divisions taking place in planes at right-angles to one another. Each segment develops a cell-wall and two flagella, and thus 2, 4, or 8 new individuals are constituted which, apart from size, resemble the parent in every respect.

This process of *asexual reproduction* is completed by the rupture or dissolution of the membrane of the parent-cell, with consequent liberation of the daughter-individuals. Since, under favourable circumstances, the succession of events just described recurs about every twenty-four hours, one individual would in the course of a week give rise to 2,097,152! Hence the often rapid appearance of such organisms in huge numbers in small bodies of water. The protoplasm of the parent is entirely incorporated in the bodies of its offspring, the dead cell-membrane alone remaining behind; thus, death from senile decay does not occur.

Under certain undetermined conditions the daughter-individuals fail to produce flagella and remain at rest within the parent cell-membrane, which gradually becomes mucilaginous (Fig. 175, H, I). The daughter-individuals assimilate and grow and sooner or later divide again, their membranes in their turn becoming mucilaginous. This may be repeated indefinitely until large gelatinous masses, enclosing numerous cells and constituting so-called *palmelloid stages* (Fig. 175, I), are produced. In the temporary adoption of this sedentary mode of life, *Chlamydomonas* and similar organisms exhibit a more marked resemblance to the majority of plants. On the return of favourable conditions, the individual cells acquire flagella and, escaping from the enveloping mucilage, resume the motile condition.

For a long time multiplication may be purely asexual, but sooner or later—usually when growth is checked—another method of reproduction sets in. This too is accompanied by division, but the resulting segments are more numerous, 16 or even 32 being formed; these are liberated as *sexual cells* or *gametes* (Fig. 176, A), which only differ from ordinary individuals in being considerably smaller and usually naked (*i.e.* devoid of a cell-wall). They move for a short time, but soon meet in pairs, and thereafter a gradual fusion (Fig. 176, B) of the two protoplasts and of their nuclei takes place. There results a single cell (termed a *zygote*) which moves for a brief period with the aid of its four flagella and then

comes to rest. The flagella are withdrawn, the protoplast assumes a spherical shape and secretes a thick stratified membrane, and copious reddish oil appears in the cytoplasm. This body (Fig. 176, C, D), known as a *zygospore*, sinks to the bottom and enters upon a resting condition.

The process of reproduction just described is known as a sexual

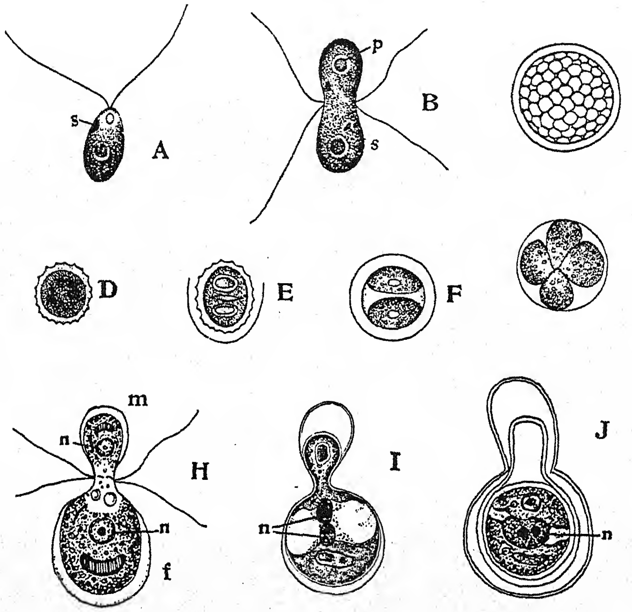


FIG. 176. Sexual reproduction of *Chlamydomonas*. A, Gamete of *C. reinhardi*. B, Stage in fusion; and C, zygospore of same. D, Zygospore of *C. ehrenbergii*; and E–G, its germination. H, Sexual fusion in *C. braunii*. I, J, Later stages of same. *f*, macrogamete; *m*, microgamete; *n*, nucleus; *p*, pyrenoid; *s*, eye-spot. (All after Goroschankin.)

one since, as in all such processes, the fusing together of two distinct individuals is involved. Despite the fact that the gametes are outwardly all alike there is evidently some internal (probably chemical) difference between them, for it is generally only gametes derived from distinct parent-individuals that fuse. In one species of *Chlamydomonas* (*C. braunii*), however, sexual union always takes place between gametes which differ both in size and behaviour. Some, produced by few divisions of an individual, are large (macro-gametes, Fig. 176, H, *f*), relatively sluggish in their movements, and soon come to rest (although the flagella persist), whilst others, formed by numerous divisions in the parent-cells, are small and

quick-moving microgametes (Fig. 176, H, *m*). The zygote is produced by one of the latter approaching a passive macrogamete and fusing with it (Fig. 176, H–J).

This kind of sexual union in which the two gametes are unlike is described as *anisogamous*, in contrast to the *isogamous* fusion of similar gametes, found in the majority of species of *Chlamydomonas*. Since in higher forms of plants, where the differentiation between the gametes is more extreme, the female are motionless and the male alone motile, the state of affairs obtaining in *C. braunii* can be regarded as a simple phase of differentiation of sex.[1]

Prolonged desiccation and extremes of temperature leave the thick-walled zygospores unharmed, even when the pool dries up. As the caked mud flakes and becomes powdery, both it and the zygospores are whirled away in windy weather as dust. If the zygospores are moistened, their colour sooner or later changes to green, owing to the absorption of the reddish oil, and the contents divide successively into a small number of parts (Fig. 176, E–G) which are liberated as new organisms by the bursting of the thick membrane. It is in this way that *Chlamydomonas* and similar forms reach, and develop in, almost any suitable piece of water.

The genus *Carteria*, individuals of which are not infrequent in fresh-water, resembles *Chlamydomonas* in all essential respects, except for the possession of four flagella (Fig. 177, F). Another motile unicellular form, commonly found in small pools of water, is variously known by the generic names *Sphaerella* and *Hæmatococcus*. Here the protoplast is separated from the firm bounding membrane by a wide transparent layer of mucilage which forms the inner part of the thick wall. This mucilage is traversed by a number of, usually branched, thread-like prolongations of the protoplast extending up to the surface layer (Fig. 177, A, C), and comparable to the cytoplasmic strands in the pits of higher plants. The peripheral region of the cytoplasm is occupied by an ill-defined chloroplast (Fig. 177, D, *c.*), containing a number (2–8) of scattered pyrenoids (*p.*), and bearing an eye-spot (*s.*) near the front end. The contractile vacuoles (Fig. 177, E) are usually numerous and irregularly distributed.

The individuals of *Sphaerella* often contain a bright red pigment which appears particularly when, with the withdrawal of the flagella and formation of a new membrane, the individuals round off to form characteristic resting-stages (Fig. 177, B). If these occur in quantity they may lend a deep red colour to the water or

[1] *C. braunii* is peculiar in having gametes provided with a cell-membrane (Fig. 176, H), a feature also seen in a few other unicellular plants, although in all other members of the Vegetable Kingdom the sexual cells are naked.

mud. The reproduction of *Sphaerella* is similar to that of *Chlamydomonas*.

Chlamydomonas, *Carteria*, and *Sphaerella* are but representatives of a whole class of simple green plants, all of which swim about like animals during the greater part of their life, and most of which

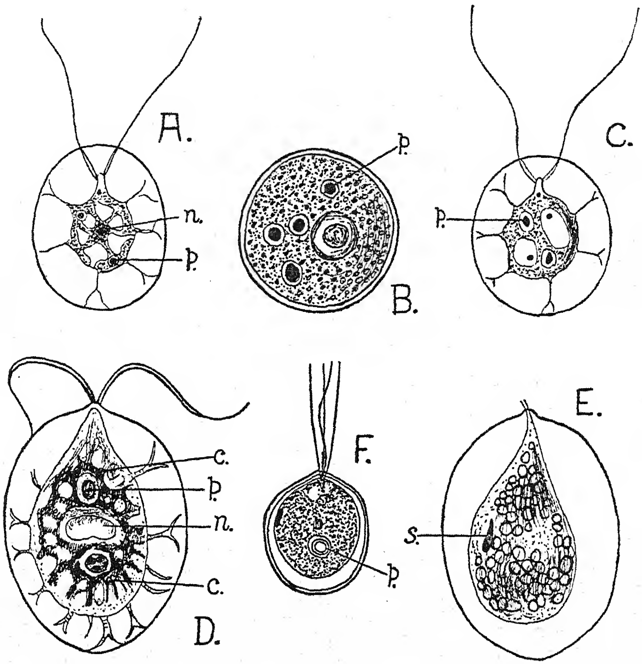


FIG. 177. *Sphaerella* (*Hæmatococcus*). A and C, *Sphaerella pluvialis*, motile individuals (after Schmidle). B, D, and E, *S. droebakensis* (after Wollenweber). B, Resting cell; D, single individual in optical section, showing the chloroplast (*c.*); E, the same, in surface-view, showing the numerous contractile vacuoles. F, An individual of *Carteria* (after Takeda). *n.*, nucleus; *p.*, pyrenoid; *s.*, eye-spot.

are inhabitants of fresh-water. In their mode of nutrition, however, they are altogether plant-like, and there is no justification for placing them in the Animal Kingdom.

There are many different kinds of *Chlamydomonas*, all of which possess two flagella, a pair of contractile vacuoles, a relatively thin cell-wall, and an oval or spherical form. These are the so-called *generic characters*, while the species differ among themselves in respect to such features as the form of the chloroplast, the presence or absence of pyrenoids, etc. (cf. Fig. 175, A, B). The genus

Sphaerella differs in the thick wall traversed by cytoplasmic processes. Generic and specific characters cannot be defined, since the degree of difference that justifies the placing of an organism in a separate genus is a matter of judgment and depends on a competent knowledge of the group concerned.

In other genera the unicellular individuals are combined in different ways to form *colonies*. Such is *Eudorina* (Fig. 178, A), which is often to be found among the slimy growth covering submerged parts of higher aquatics. The colony commonly consists of 32 globular cells embedded at regular intervals in the

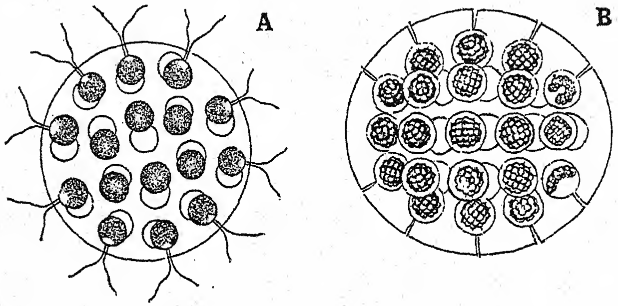


FIG. 178. *Eudorina elegans*. A, Vegetative colony; the flagella are seen on ten of the individuals. B, A colony showing asexual reproduction, the daughter-colonies in various stages of development. (A, after West; B, after Hartmann.)

peripheral portion of a spherical or oval mass of mucilage. Each individual cell is almost identical in structure with a *Chlamydomonas*-plant, the two flagella projecting well beyond the mucilage-investment, and often being easily recognisable where they traverse the latter (Fig. 178, A). By the united action of the flagella of all the individuals, the whole colony rotates rapidly through the water. Reproduction is usually effected by the subdivision of each of the constituent cells to form as many small *daughter-colonies* (Fig. 178, B), which are subsequently liberated by the breaking down of the mucilage-investment of the parent. Not uncommonly associated with *Eudorina* are the plate-like colonies of *Gonium* (Fig. 180, D).

The spherical colonies of *Volvox* are far more elaborate. Since they are composed of several thousand cells, they are of quite appreciable dimensions (usually about the size of a pin's head) and readily visible to the naked eye (Fig. 179, A, B). The constituent cells (Fig. 179, C, D) often show more resemblance to *Sphaerella* than to *Chlamydomonas*, since they have thick mucilaginous walls (*m*) traversed by protoplasmic processes, which

correspond in adjacent individuals (cf. p. 57). Movement is effected, as in *Eudorina*, but flagella are lacking from a few large cells (Fig. 179, A, *d*) located in the part of the colony directed backwards during movement. It is these large cells alone that divide to form daughter-colonies, the latter being at first liberated

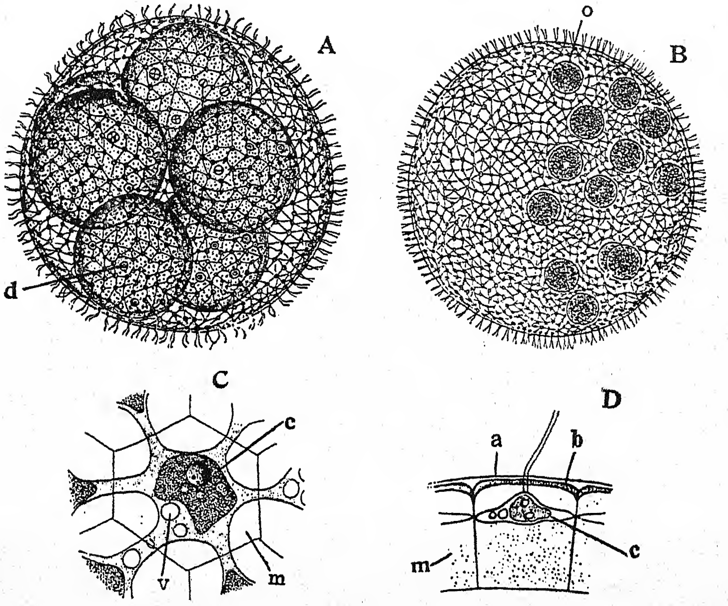


FIG. 179. Structure of *Volvox*. A, B, *V. aureus*. A, Colony enclosing five daughter-colonies, the latter already exhibiting the large cells (*d*) from which another generation will be developed. B, Female colony with mature oospores (*o*). C, Surface-view; and D, section of single cells of *V. globator*. *a*, *b*, external layers of wall; *c*, chloroplast; *m*, mucilage of cell-wall; *v*, contractile vacuole. (A, B, after Klein; C, D, after Meyer.)

into the hollow interior of the parent (Fig. 179, A), where they grow until set free by its rupture.

Volvox thus affords a simple example of the setting apart of certain cells for special purposes; most are purely vegetative and perish with the death of the parent, whilst a few are destined to undergo division and persist as daughter-colonies. This is in marked contrast with *Eudorina*, where every cell is generally capable of performing *all* the life-functions (nutrition, growth, reproduction, etc.). The specialisation exhibited by *Volvox* brings with it the death of the greater part of the colony, a feature which is generally associated with division of labour. *Eudorina* and

Volvox also exhibit an advanced type of sexual reproduction, analogous to the oogamy described on p. 306 (cf. Fig. 179, B).

A large proportion of the simple unicellular and colonial green plants are, however, non-motile throughout the vegetative phase

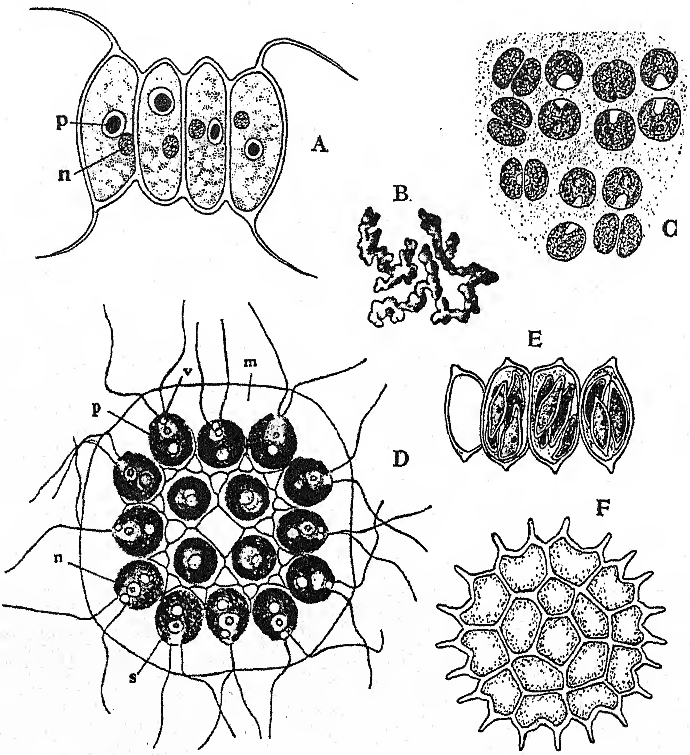


FIG. 180. Various colonial Green Algæ. A and E, *Scenedesmus quadricauda*; in E, the individuals are producing daughter-colonies. B, C, *Tetraspora*; B, a colony approximately natural size; C, a small part, much enlarged. D, *Gonium pectorale*. F, *Pediastrum*. *m*, mucilage; *n*, nucleus; *p*, pyrenoid; *s*, eye-spot; *v*, contractile vacuole. (A, after G. M. Smith; B, after West; C, after Reinke; D, after Hartmann; E, after Senn.)

of their life-history, and only exhibit movement, if at all, in connection with reproduction. They thus recall the palmelloid stages of *Chlamydomonas*, to which some, indeed, show considerable resemblance, *e.g.* the bright green gelatinous masses of *Tetraspora* (Fig. 180, B), commonly found in spring in small ponds, and containing numerous cells arranged in groups of four (Fig. 180, C).

As an example of a motionless unicellular plant, the widely

distributed *Pleurococcus*, which commonly forms the green powdery covering on tree-trunks, palings, etc., may be studied. Under the microscope the green powder is seen to consist of small groups of 2, 4, or rarely more, cells, intermingled with which are more or less numerous rounded individuals (Fig. 181, A), all representing different stages of *Pleurococcus*. Each cell has a moderately thick wall, and contains a single nucleus and a lobed chloroplast (Fig. 181, B). The isolated cells constitute the adult form, and sooner or later divide, commonly by two successive walls at right angles to one another, to form four-celled packets. Each daughter-cell is thus the quadrant of a sphere, but with subsequent growth it rounds off and separates from its neighbours, giving rise again to the adult form. This process of vegetative propagation is, when conditions are favourable, repeated at frequent intervals, and in this way *Pleurococcus* rapidly covers large areas.[1]

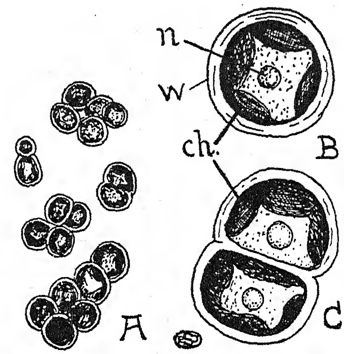


FIG. 181. *Pleurococcus*. A, Group of cells, under the low power. B, Single cell, and C, pair of cells, under the high power. *ch.*, chloroplast; *n*, nucleus; *w*, cell-wall.

The ordinary cells of *Pleurococcus* possess a remarkable power of withstanding drought, almost comparable to zygospores such as those of *Chlamydomonas* and other simple forms in which the vegetative cells are extremely susceptible to adverse conditions. Thus *Pleurococcus* can exist, and even flourish, in the exposed dry habitats that it usually frequents, and its specialisation for this habitat is evidenced by its inability to survive prolonged submergence. Although retaining its normal green appearance throughout the year, its activities are more or less completely arrested during prolonged periods of drought, when its only source of moisture is inadequate dew.

Many of the motionless colonial green forms are common in fresh-water pools where they occur entangled among the filaments of the pond-scums or in the slimy growth on the surface of larger water-plants. As examples we may mention the four- or eight-celled colonies of *Scenedesmus* (Fig. 180, A), and the characteristic

[1] Intermingled with the cells of *Pleurococcus* one often finds other spherical cells of about the same size, which differ in possessing a central lobed chloroplast with a prominent pyrenoid. These belong to the terrestrial Alga *Trebouxia* (*Cystococcus*), which plays a part in the formation of many Lichens (p. 342).

disc-like plates of *Pediastrum*, in which particularly the marginal cells are often of very distinctive form (Fig. 180, F). In both, the ordinary course of reproduction consists in the division of the contents of each cell to form a new colony (cf. Fig. 180, E).

Forms like *Scenedesmus*, *Pediastrum*, *Eudorina*, etc., together with many of the unicellular Diatoms and Desmids to be mentioned in the next chapter (pp. 294, 296), very commonly occur in considerable numbers floating freely in the surface-layers of lakes, rivers, etc. (Fig. 182). A similar *plankton* occurs abundantly in most seas, and these microscopic plants form the food for many aquatic animals and probably provide essential vitamins. They may at times occur in such prodigious quantity as to lend a visible colouration to the water, a phenomenon especially seen in fresh water and spoken of as "waterbloom"; for this the Blue-green Algæ (p. 293) are most frequently responsible. It may be added that the character of the plankton usually differs markedly in different seasons of the year.

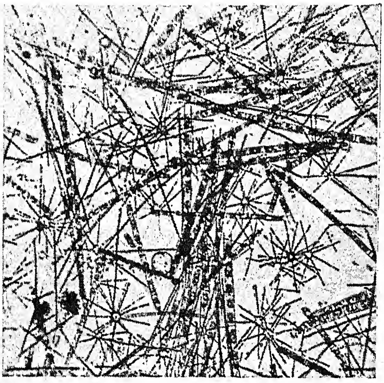


FIG. 182. Photograph of freshwater Diatom-Plankton; the two principal forms present are the filamentous *Melosira*, and the star-shaped colonies of *Asterionella* (from Wesenberg-Lund).

The Vegetable Kingdom taken as a whole comprises sedentary organisms, and consequently the capacity for free movement has come to be regarded as an essentially animal characteristic. But the motile habit has been seen to occur in quite a considerable number of unicellular and colonial aquatic plants, and is by no means confined to them, being observable also among higher forms (*e.g.* Mosses, Liverworts, Ferns, etc.), although here restricted to the male reproductive cells. The power of movement cannot therefore serve as an invariable distinction between the two Kingdoms.

Nevertheless the Vegetable Kingdom may be described as essentially sedentary, and the Animal Kingdom as essentially motile. This distinction may be related to the necessity for animals to move from place to place in search of food, whilst plants, depending as they do almost solely on simple chemical compounds, can best obtain these by being stationary. It will, for instance, be clear that, for the terrestrial plant, the intimate contact which is

necessary between root and soil is totally inconsistent with a motile habit. Another distinction between higher plants and animals is the possession by the latter of highly developed sense-organs. This too can probably be related to the motile habit, with the concomitant necessity for rapid response to the ever-changing conditions of the environment. It is significant that in animals like the Hydrazoon *Obelia*, which have a motile and sedentary phase in their life-history, the more specialised organs of sense occur in the former.

Contractile vacuoles and eye-spots are found alike in many lowly plants and animals, and cannot be said to be characteristic of either. In fact, the only satisfactory criterion as to the inclusion of an organism in the one Kingdom or the other is the method of nutrition. Plants absorb their food in liquid or gaseous form, and, with the exception of those lacking chlorophyll, build up their bodies from simple inorganic compounds; animals feed on complex organic substances, and take up a large part of their food in the solid state.

The most important distinction between the two Kingdoms thus depends on the presence or absence of chlorophyll. There are many organisms, however, which, as comparative study shows, possess the characteristics of plants, but which are colourless saprophytes (p. 315). Some green plants can even ingest solid food. Just as it is amongst the simple unicellular plants and animals that we find the closest resemblances, so too it is the complex organisms of the highest groups, as exemplified by Flowering Plants and Mammals, that exhibit the greatest distinction and portray the salient plant and animal characters in the most marked degree.

CHAPTER XXVI

SEAWEEDS AND OTHER ALGÆ

THE organisms considered in the last chapter belong to a group of simple plants termed *Algæ*,[1] which also include Seaweeds and many fresh-water species. The Algæ, with very few exceptions, possess chlorophyll and their nutrition is like that of other green plants. They are distinguished mainly by the relatively simple construction of their body, which varies from a single cell to a multicellular thallus of some complexity, and by the usually unicellular character of their reproductive organs.

The simplest type of multicellular plant-body is a filament or row of cylindrical cells, all nearly identical, both in structure and function. Examples are furnished by *Ulothrix* (Fig. 194, A), *Spirogyra*, and *Œdogonium*, genera whose species commonly occur as floating tangled masses in ponds and stagnant ditches, although some are found in flowing water. Every cell is generally capable of division, but in *Œdogonium* this is restricted to occasional cells, recognisable by the presence, at one end, of a succession of fine rings (known as caps), formed singly at each division (Fig. 195, C, H).

The habit of the plant becomes slightly more complex when the filaments are branched, as in *Cladophora* (Fig. 183, A, B) and *Ectocarpus* (Fig. 197, B, C). Species of the latter commonly occur as brown tufts or tresses attached to diverse substrata in the rock-pools on the seashore, whilst those of the former, though also found in similar situations, are common in well-aerated fresh-water. Each branch of a *Cladophora* (Fig. 183, B) terminates in an elongated apical cell, with specially dense contents. These cells constitute *growing points*, by whose enlargement and division the branches gradually lengthen, the segments cut off from them not uncommonly undergoing no further division. Branching originates by the outgrowth from the upper ends of the cells, just beneath the septa, of small protrusions which are cut off to form the apical cells of the new branches (Fig. 183, B); the degree of branching varies greatly in the different species and even in different individuals.

[1] For reference-books, see p. 314.

The lower cells of the main *Cladophora*-filament put out thread-like organs of attachment (rhizoids), which have scanty contents, and

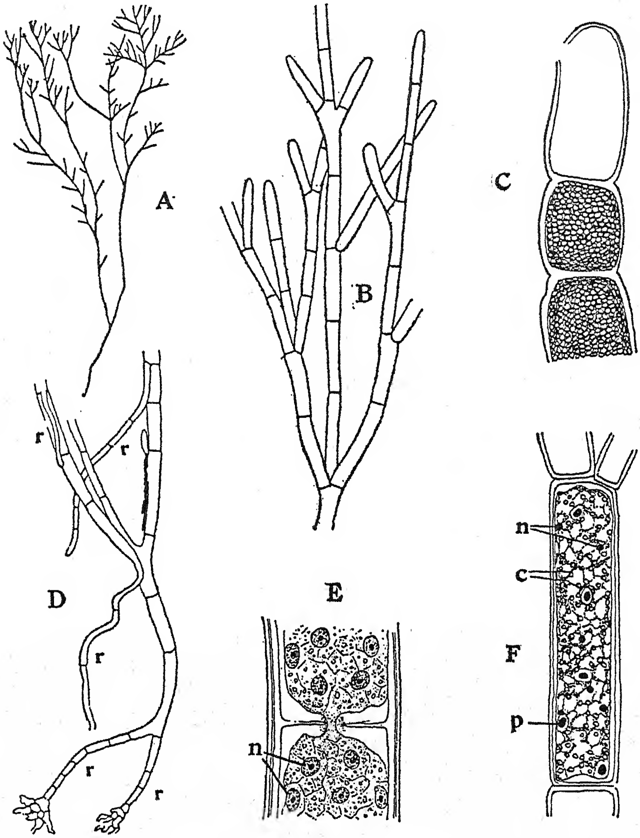


FIG. 183. *Cladophora*. A, Small part of a plant of *C. glomerata* (natural size, after West). B, The same, enlarged (after Migula). C, Apex of a branch with three zoosporangia, the top one having liberated its contents through the aperture seen on one side (after Oltmanns). D, Base of plant, showing the attaching rhizoids (*r.*) (after Brand). E, Small part of a cell showing the manner of ingrowth of the septum (cf. p. 58) separating two daughter-cells (after Strasburger). F, Single cell stained to show nuclei (*n.*), pyrenoids (*p.*), and the net-like chloroplast (*c.*) (after Weltstein).

are often branched (Fig. 183, D, *r*). In the young stages of most filamentous Algæ the basal cells are specially modified for attachment (Fig. 195, G), but in *Spirogyra*, *Œdogonium*, and *Ulothrix* the filaments usually break off and become free-floating as they grow older, except in species which inhabit flowing water. The

lobes of the attaching cells grow into all the irregularities of the substratum, to which they cling after the manner of a sucker, adhesion being often increased by the secretion of a cementing substance. The great efficiency of the attaching cells is very evident in those species of *Cladophora* which grow on wave-beaten rocks or in rapidly flowing streams.

FIG. 184. Photograph of part of a plant of the Green Alga *Draparnaldia*, seen under the low power of the microscope. [Photo. E. J. S.]

The frequent restriction of the power of division to the terminal cells of *Cladophora* marks a considerable step in division of labour as compared with *Ulothrix*. This is also seen in the formation of reproductive units, which are almost confined to the cells of the lateral branches (cf. p. 301). A more extreme condition is seen in *Draparnaldia* (Fig. 184), which is not uncommon in slowly flowing water. Here the main axes, which serve almost solely for support, consist of large cells with small chloroplasts, whilst photosynthesis and reproduction are relegated to the densely branched laterals.

Division of labour is also well marked in *Ectocarpus*, where the thallus usually exhibits a differentiation into upright and prostrate portions (Fig. 197, B), both of which are branched and filamentous, the latter acting as the organ of attachment. The ends of the branches often consist of almost colourless tapering cells.

A very unusual type of thallus is that of *Vaucheria*, the species of which form rather coarse dark green wefts on damp soil or in fresh or salt water. The branched filaments, though of considerable width and length, lack septa (Fig. 196, A), and might as a consequence be regarded as consisting of single cells. Since, however, each contains numerous nuclei (Fig. 196, D, *n*.), it is better

compared with a multicellular organism where too the cytoplasm exhibits continuity (cf. p. 57), but where mechanical support is afforded by the walls separating the uninucleate portions. The filaments of *Vaucheria* depend for their rigidity entirely upon turgor, and very readily collapse after injury.

At low tide on rocky shores one often sees thin crinkled slimy

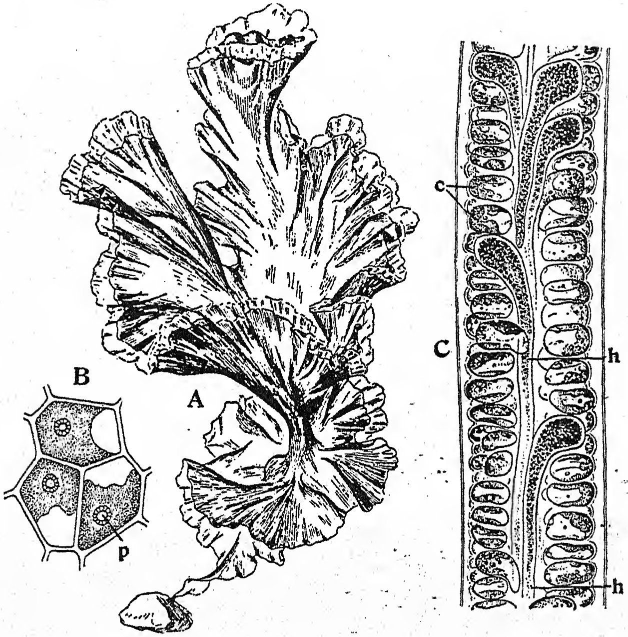


FIG. 185. *Ulva lactuca.* A, Habit. B, A few cells in surface-view. C, Section of thallus. *c*, chloroplast; *h*, attaching rhizoids; *p*, pyrenoid. (B, after Schimper; the rest after Thuret.)

sheets of a vivid green colour which are the Alga *Ulva* (the Sea Lettuce) (Fig. 185, A). The large thallus consists of two superposed layers of cells of a uniform character throughout (Fig. 185, C) except where they grow out into rhizoids (*h*) which form the attaching base. Very young plants of *Ulva* begin as a simple unbranched filament, whose cells, however, soon undergo division in several directions to produce the flat thallus.

Most of the genera hitherto studied are so-called Green Algæ (*Chlorophyceæ*), the majority of which inhabit fresh-water. Most Seaweeds, however, are brown or red owing to the presence of special pigments in the chloroplasts masking the chlorophyll. The colouring matters are readily extracted with water from dead

specimens, which then assume a green colour. Diverse functions have been attributed to these pigments.

Many Brown Seaweeds (*Phæophyceæ*), of which *Ectocarpus* (Fig. 197, B) has already furnished a relatively simple example, are far bulkier than any Algæ yet noticed, and evince marked division of labour. Thus *Laminaria*, which occurs near low-tide level, has a thallus consisting of three distinct regions (Fig. 189*): viz. a richly branched holdfast, by which the Alga is anchored to rocks, a long, stout cylindrical stalk which may be as much as an inch in diameter, and a correspondingly large leathery blade. The latter either takes the form of a broad ribbon (*L. saccharina*) or of a deeply divided frond like the palm of a hand (*L. digitata*, Fig. 189*). Whilst the stalk and attaching organ are perennial, the blade is renewed, usually in the spring of each year, by means of a small-celled meristem situated at the top of the stalk; the new frond therefore appears at the base of the old one, which eventually becomes detached by the action of the waves. The holdfast is composed of numerous cells with thick gelatinous walls, and develops additional branches suggestive of prop-roots as the plant grows older, whilst simultaneously the stalk slowly increases in thickness.[1] A related form, *Chorda*, has whip-like hollow thalli, a yard or more long.

The Seaweed *Macrocystis*, which is a close ally of *Laminaria* and particularly common in the Southern Hemisphere, attains to enormous dimensions, often measuring as much as 200 feet from end to end.

The commonest Brown Alga is the Bladder Wrack (*Fucus vesiculosus*, Fig. 187, B), which is found on rocks between tide-levels, so that it is uncovered for several hours at a time (Fig. 186). An entire plant often attains a length of from one and a half to three feet, and exhibits three regions similar to those of *Laminaria*, but the stalk is short and the frond repeatedly forked (Fig. 187). Such forked branching is common among the simpler plants and is termed *dichotomy*; it results from a halving of the apical cell. Each portion of the thallus possesses an obvious midrib (*m.*), which is thicker and more pronounced in the older parts where it gradually passes over into the stalk. The latter is indeed nothing else than the persistent midrib of the first-formed part of the thallus. The holdfast is a sucker-like disc composed of many cells.

In a narrow pocket at the tip of each branch of the frond is an apical cell, the segments of which divide to form the tissue of the

[1] This Alga not infrequently develops on rock-fragments that are too small to anchor the adult, in consequence of which the thalli and attached rocks get carried out to sea. This may sometimes take place on a considerable scale.

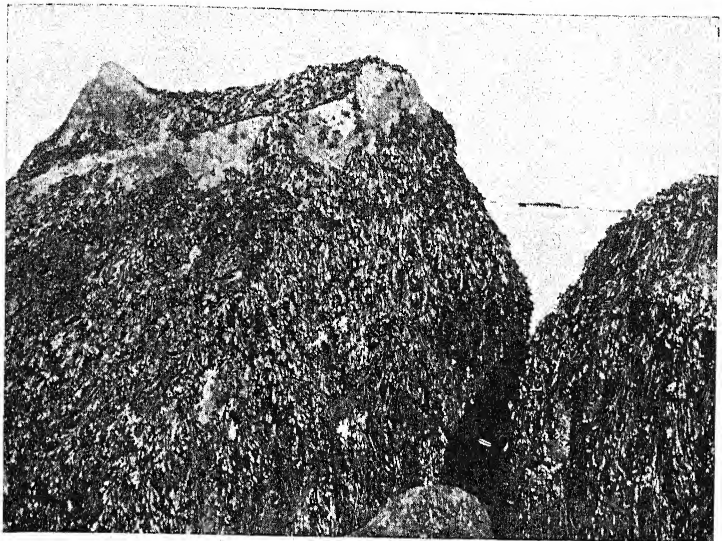


FIG. 186. Photograph of *Fucus vesiculosus* on rocks between tide-levels. [Photo. E. J. S.]

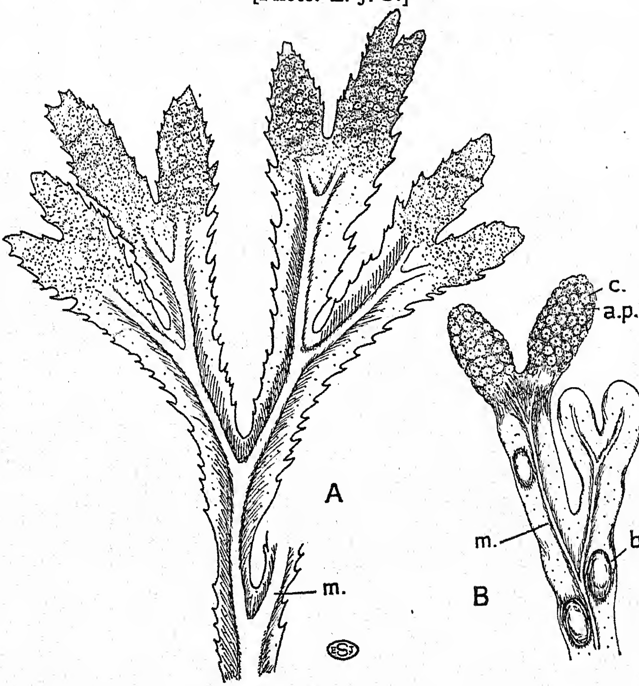


FIG. 187. *Fucus*. A, Part of a thallus of the Serrated Wrack (*F. serratus*). B, Ditto of the Bladder Wrack (*F. vesiculosus*); fertile apices are evident in both. *ap.*, aperture of conceptacle (*c.*); *b.*, air-bladder; *m.*, midrib of thallus.

thallus. The paired air-bladders (Fig. 187, B, *b.*), which appear as occasional large swellings on either side of the midrib, and to which the specific name is due, increase the buoyancy of the plant when submerged, and may also, like the air-canals of aquatic Flowering Plants, serve for purposes of respiration.

Scattered irregularly over the whole surface of the frond are slightly protruding dots marking the positions of small spherical cavities (*conceptacles*) in the thallus. These are lined with hairs which mostly project as a minute tuft through the tiny aperture leading to the exterior. Usually some of the branches of the frond have swollen ends (Fig. 187) provided with much more conspicuous (fertile) conceptacles (*c.*) enclosing the sexual reproductive organs (cf. p. 310).

The Serrated Wrack (*Fucus serratus*), which is almost as common on rocky shores, is distinguished by the toothed margin of the frond, the absence of air-bladders, and the less distinct swelling of the ends bearing the fertile conceptacles (Fig. 187, A).

A transverse section through the frond of any *Fucus* (Fig. 200, B, p. 310) presents three regions. At the outside is a small-celled photosynthetic zone (*a.*), of which the most obvious part is the palisade-like surface-layer whose cells show occasional tangential division-walls. The cells of the central medulla (*m.*) are conspicuous for their thick mucilaginous walls, by which the small protoplasts are widely separated. The elements in question, whose function is partly mechanical and partly conducting, are of considerable length, but roughly follow the direction of the thallus, and hence appear more or less oval in transverse section. Between the medulla and the surface region is a cortex of relatively large storage-cells (*S.*) with highly refractive contents that are presumably products of photosynthesis. The outermost layer of the thallus is meristematic and adds to the photosynthetic region, whose innermost cells gradually enlarge to form elements of the cortex. Similarly the medulla slowly increases at the expense of the adjacent storage-cells, so that, although there is an obvious differentiation into three regions, the same cells may perform different functions in successive periods of the life of the thallus.

In the region of the midrib the structure is more compact owing to the presence of numerous additional elements formed from thread-like outgrowths arising from the cortical cells and pursuing in the main a longitudinal course through the mucilage of the medulla. The thick midribs of older parts are due not only to the large number of elements of this kind that are present, but also to a secondary meristematic activity in the region of the cortex. Despite the diversity of form of the cells, there is not

the marked differentiation in the character of the walls which is found in higher plants.

A cross-section of the stalk or frond of *Laminaria* shows essentially the same construction, and here the high specialisation of the Brown Algæ is evidenced by the presence of sieve-like areas, analogous to those of sieve-plates, on the cross-walls of many of the elongated elements of the medulla. Similar structures occur in *Fucus*, but are not so easily recognised.

Clothing the rocks, which for the greater part of the season are only reached by spray, one finds the Seaweed *Pelvetia*, which, though closely allied to *Fucus*, is much smaller, and in which the swollen fertile ends are a particularly conspicuous feature (Fig. 188).

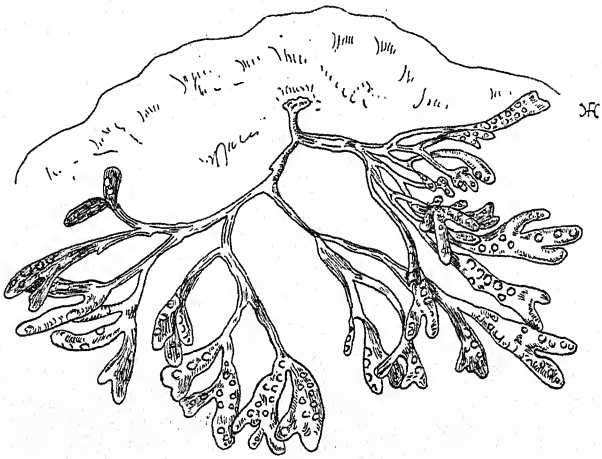


FIG. 188. Plant of *Pelvetia canaliculata*, about natural size, showing the basal attaching disc and the prominent fertile conceptacles.

The structure of the thallus shows no important differences, but the branches of the frond are much narrower and channelled on their upper surface, features which aid in the retention of moisture; moreover, the thallus is thus mainly illuminated by oblique light, so that the heating effect of the sun, and therefore transpiration, is presumably diminished during the hot hours of the day. The principal differences exhibited by *Pelvetia* can therefore be related to the special conditions of its habitat.

On rocky shores the Brown Algæ *Pelvetia*, *Fucus*, and *Laminaria* often form three zones at successively lower levels, occurring in the order named. Other members of the group are free-floating, as, for example, some species of *Sargassum* (Fig. 189), huge stretches of which characterise the Sargasso Sea in the Mid-Atlantic. Some

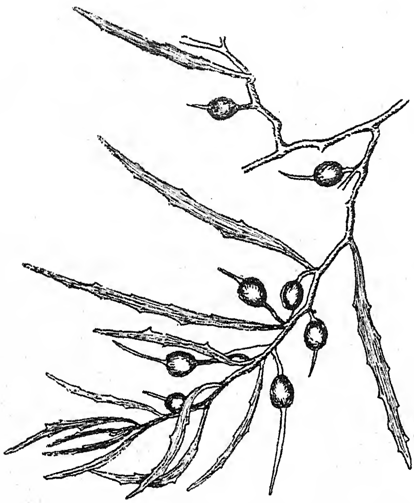


FIG. 189. Part of a plant of *Sargassum*, about natural size, showing numerous air-bladders.

of the larger Brown Algæ are edible, and indeed extensively cultivated in Japan, whilst in the West of Scotland *Fucus* and similar forms are abundantly used as manure.

Most of the Red Algæ (*Rhodophyceæ*) are much smaller plants preferring weakly illuminated habitats, so that they either grow at considerable depths below low-tide level or in shady rock-pools. In many the thallus is a branched thread (e.g. *Polysiphonia*, *Ceramium*, Fig. 190, C), whilst in others it is flattened (*Chondrus*, Fig. 190, A). In the former the larger branches usually consist of several rows of cells, whilst in the latter a number of distinct tissue-regions can often be distinguished. A red alga, often abundant in rock-pools, is *Corallina* (Fig. 190, B), whose branched thallus is composed of numerous segments loosely jointed to one another, and densely encrusted with carbonate of lime, giving it a pinkish-white colour. Similar *calcareous Algæ*, often of larger dimensions, are common in tropical seas, where they frequently play an important part in the production of coral-reefs, and comparable forms are known in the past to have contributed largely to the formation of certain limestone rocks. Diverse tropical Red

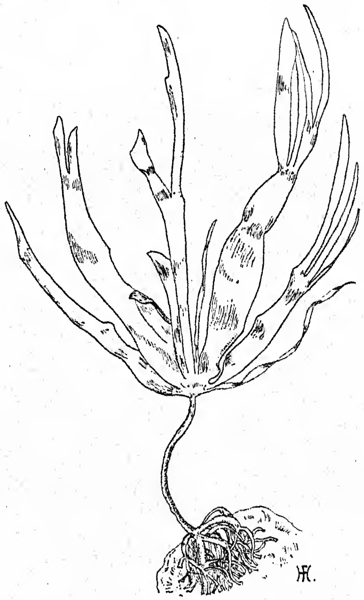


FIG. 189 *. Young plant of *Laminaria digitata*, about one-fifth natural size.

Algæ are the source of agar-agar, a substitute for gelatine extensively used for bacterial cultures, whilst Carrageen (*Chondrus crispus*, Fig. 190, A) furnishes a valuable invalid diet.

There is still another large group of Algæ (*Cyanophyceæ*) named after the prevailing blue-green colour. These, though relatively rare in the sea, are common in fresh-water, and often particularly characteristic of damp terrestrial habitats, such as rocks exposed to a constant trickle. Their great adaptability to varied conditions is also shown by their playing the leading rôle alike in the vegetation of hot springs and in the frigid lakes of the

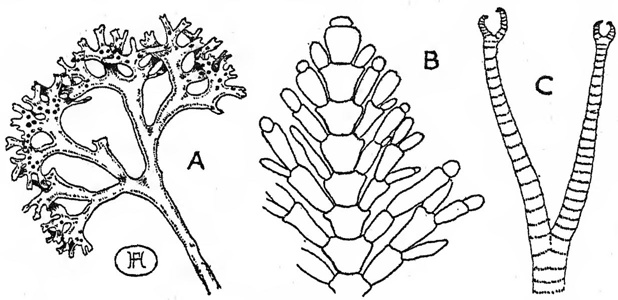


FIG. 190. Rhodophyceæ. A, *Chondrus crispus*, with tetraspores. B, *Corallina*. C, *Ceramium*. (B and C enlarged.)

Antarctic continent. The Blue-green Algæ are either colonial (*Glœocapsa*, Fig. 191, C), or filamentous (*Oscillatoria; Lyngbya*, Fig. 191, F; *Nostoc*, Fig. 191, B). The cells possess either no nucleus in the ordinary sense, or one of very simple construction, and the pigments are diffused through the peripheral cytoplasm. The cells or filaments are often contained in large numbers in mucilaginous envelopes (e.g. *Glœocapsa*, *Nostoc*), to which and to the absence of vacuoles may be probably attributed the capacity of many species to survive considerable periods of drought.

Common members of the group are: *Glœocapsa* forming extensive gelatinous coverings on damp substrata (Fig. 191, C); *Oscillatoria* and *Lyngbya*, whose undifferentiated and unbranched filaments of discoid cells (Fig. 191, F) occur as sheets or bundles in fresh-water pools, on moist stonework, etc.; *Tolypothrix*, a branched filamentous form, usually aquatic (Fig. 191, E); and *Nostoc*, some species of which are terrestrial. The species of *Nostoc* have the form of variously shaped gelatinous clumps (Fig. 191, B, *b*) in which are embedded numerous tortuous chains of rounded cells, interrupted here and there by slightly larger colourless ones (*heterocysts*, seen also in *Tolypothrix*, Fig. 191, E, *h*.) of uncertain

function. The Cyanophyceæ often play a very important part in nature as the first plants to colonise bare ground.

In every habitat where other Algæ occur there can usually

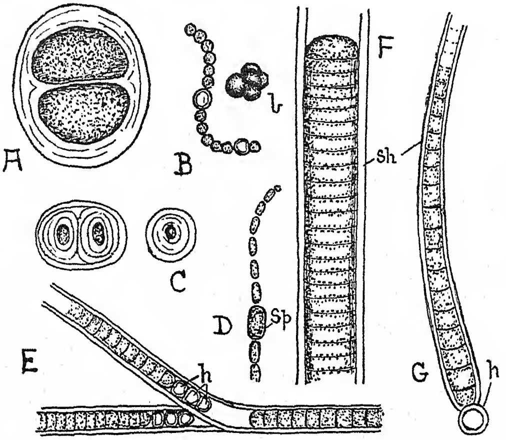


FIG. 191. Diverse Blue-green Algæ. A, *Chroococcus*. B, Single thread from colony of *Nostoc* (the colony shown natural size in *b*). C, *Glœocapsa*. D, *Anabæna* (with spore, *Sp*.). E, *Tolypothrix*. F, *Lyngbya*. G, *Rivularia*. *h*., heterocysts; *sh*., sheath.

be found unicellular forms known as *Diatoms* (Fig. 192) which possess quite special characteristics of their own. The individuals are either unattached, and then often endowed with a power of fairly rapid movement, or else fixed to the surface of larger Algæ and other aquatics. The Diatoms are brown or greenish in colour. Each plant is provided with a cell-wall richly impregnated with silica, and usually bearing a symmetrical and often highly elaborate pattern of sculptured markings (Fig. 192). With the death of the organisms the practically unaltered siliceous shells sink, so that, where Diatoms are plentiful, deposits of almost pure silica slowly accumulate at the bottom of the water. Instances are afforded by the extensive beds of "diatomaceous earth" found at Dolgelly in Wales, at Bilin in Bohemia, and elsewhere, some being of marine, others of fresh-water origin. Such deposits are utilised commercially in the preparation of dentifrices, as insulating material, and, owing to the very small size of the individual particles, for filtration. Marine Plankton at times consists almost entirely of Diatoms, and is an important source of food for fishes.

Although several groups of Algæ are designated according to the prevailing colour of their plastids, they are characterised by

many more important features, and especially by the nature of their reproductive processes (see next chapter). The *chloroplasts*, in general, assume the most complex forms among the Green Algæ, where there is often but a single one in each cell, a condition already noticed in *Chlamydomonas* and its allies (cf. p. 272). Moreover, the chloroplasts of the Green Algæ commonly possess one or more pyrenoids and, during active photosynthesis, starch is formed as a reserve-product, first around the pyrenoids, and then in the general substance of the plastid. Whilst most of the colonial (e.g. *Scenedesmus*) and less differentiated filamentous forms (e.g. *Ulothrix*) have a relatively simple undivided chloroplast, greater complexity is met with in many of the more highly organised Green Algæ.

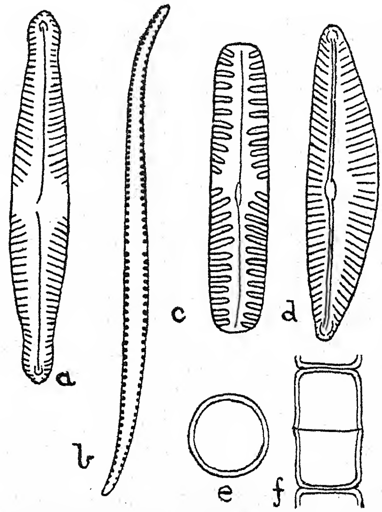


FIG. 192. Various Diatoms (only the siliceous walls are shown). *a* and *c*, *Navicula*; *b*, *Nitzschia*; *d*, *Cymbella*; *e*, end-view, and *f*, side-view of cells of the colonial *Melosira*.

The band-shaped chloroplast of *Ulothrix* has the form of a complete or incomplete cylinder (Fig. 194, A, B), occupying the lining layer of cytoplasm within the thin cell-wall; it contains one or more pyrenoids. In *Cladophora* and *Œdogonium*, on the other hand, the cylindrical chloroplast is a perforated network with numerous scattered pyrenoids. In *Œdogonium* (Fig. 195, A) the meshes are elongated and more or less parallel to one another, whilst in *Cladophora* (Fig. 183, F) the network is irregular and ill-defined. Other peculiarities of the cell-structure of *Cladophora* are the numerous small nuclei (Fig. 183, F, *n*), that are recognisable after careful staining, on the inner side of the chloroplast, and the thick stratified wall to which this Alga owes its coarse texture; the former feature is in marked contrast to the single nucleus found in the cells of *Ulothrix* and especially obvious in *Œdogonium* (Fig. 195, A, *n*).

The non-septate threads of *Vaucheria* possess numerous discoid chloroplasts which are lodged in the lining layer of cytoplasm and lack pyrenoids (Fig. 196, D, *c*); this Alga also contrasts with

other Chlorophyceæ in producing no starch, the excess food being stored as oil.

The most elaborate types of chloroplasts are found in *Spirogyra* and its allies, which belong to a group of the Green Algæ known as the *Conjugatæ*, practically confined to fresh-water. Some of these are filamentous like *Spirogyra* (Fig. 27), whose spiral chloroplasts,

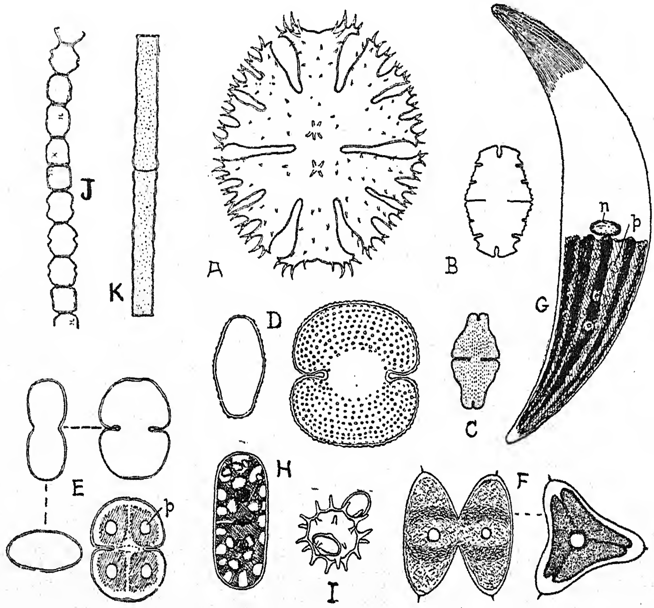


FIG. 193. Diverse Desmids. A, *Micrasterias*. B and C, *Euastrum*. D and E, *Cosmarium* (in E the top left-hand figure shows the cell in side-view; the lower left-hand figure the cell in end-view). F, *Staurastrum* (the right-hand figure shows the end-view) (after Ostenfeld). G, *Closterium*. H, *Cylindrocystis*. I, zygospore of *Cosmarium meneghinii* (after West). J, *Desmidium* (filamentous). K, *Pleurotænium*. The cell-contents are shown only in E–H. *n*, nucleus; *p*, pyrenoids.

one or more to each cell, have already been described (p. 42), and *Zygnema* (Fig. 201, F), where the cells contain two star-shaped chloroplasts with a conspicuous pyrenoid (*p.*) at the centre of each. A large number of the Conjugatæ are, however, unicellular forms, named *Desmids* (Fig. 193), which resemble *Spirogyra* and *Zygnema* in their methods of reproduction, but often have even more elaborate chloroplasts.

The Desmid-cell usually exhibits two symmetrical halves, each containing one or two chloroplasts, and not uncommonly separated by a median constriction, where the single nucleus is situated (e.g.

Cosmarium, Fig. 193, D, E). The wall is often richly sculptured or provided with spinous outgrowths (Fig. 193, A, D). In *Closterium* (Fig. 193, G), species of which are very frequent, each half of the, usually semilunar, cell is occupied by a chloroplast consisting of a central rod which contains a row of pyrenoids (*p.*) and bears a number of radiating longitudinal plates; the latter appear as dark green streaks when the cell is viewed from the surface. The small vacuoles, commonly seen at either end of the cell, enclose minute crystals of gypsum exhibiting Brownian movement, and are a peculiar feature of this genus. Similar elaborate chloroplasts are found in *Cosmarium* (Fig. 193, E) and *Micrasterias* (Fig. 193, A).

The extreme variety of the chloroplasts amongst the Algæ is in striking contrast with their comparative uniformity amongst Flowering Plants. It may be remarked, however, that the chloroplast of the simple Alga is as much the photosynthetic organ as is the leaf in the higher plant, where, too, a great diversity of structure in an apparently uniform habitat is found.

The Algæ afford an excellent illustration of the fact that *division of labour* is associated with increased complexity of structure. In many filamentous Green Algæ all the cells, except that serving for attachment, may be alike in form and play an equal part in growth and division (e.g. *Ulothrix*, *Spirogyra*). At the other extreme the large Brown Algæ not only exhibit a relegation of attachment, growth, and reproduction to definite parts of the thallus, but the units of which the latter is built up also show a certain specialisation into conducting, photosynthetic and meristematic elements.

It is probable that the complex type of cell arose from a much simpler one, and that similarly the multicellular organism had its origin in the unicellular, as is usually the case in the course of the individual development. High efficiency for particular conditions of life demand complexity of structure which, however, like all specialisation tends to diminish the adaptability of the organism, to reduce its capacity for meeting changed conditions. It is in harmony with this that only a small part (viz. the relatively unspecialised reproductive cells) of highly specialised organisms persists from one generation to the next, whereas in a simple organism the whole may survive in the bodies of its offspring. Herein the more highly differentiated forms exhibit a provision whereby the next generation is temporarily relieved of the trammels of the specialisation of its parents, and thus probably becomes better fitted to meet the extremely varied conditions to which the different individuals are subjected during their development.

The diverse Algæ are not found in equal quantity all the year

round, many disappearing more or less completely during the warmer months or during the winter. The different species of fresh-water Algæ frequently succeed one another, showing a *periodicity* which is probably conditioned by a multiplicity of factors, of which temperature and illumination are probably among the most important. Some forms (e.g. *Cladophora*), however, are encountered all the year round, although in varying abundance.

CHAPTER XXVII

REPRODUCTION OF THE ALGÆ

JUST as the vegetative structure of the Algæ shows progressive stages in complexity, so also do the processes of reproduction, although specialisation in the one respect does not always go hand in hand with specialisation in the other. Thus *Cladophora*, with its markedly differentiated vegetative system, shows simple reproductive processes, similar to those of *Ulothrix*.

At times of active growth *Ulothrix* reproduces vegetatively by the mere breaking or *fragmentation* of its filaments into short lengths which develop into new threads. Not infrequently, however, a more specialised mode of multiplication obtains, which is spoken of as *asexual reproduction* owing to its general resemblance to the sexual method except for the absence of fusion. Both the sexual and asexual reproductive cells are motile, although the ordinary *Ulothrix*-filament is without any power of movement.

Asexual reproduction may take place in some or all of the cells of a filament. At its commencement, the protoplasts round off slightly and thereupon usually divide, along successive planes at right angles to one another, into 2, 4, or even 8 separate parts, the number depending upon the size of the cell (Fig. 194, C). The products of division (*sp*), each of which has a chloroplast and pyrenoid of its own, are liberated through a small round hole formed in the side-wall, but remain enveloped for a few seconds in a thin bladder of mucilage (Fig. 194, C). Meanwhile each portion has developed four flagella, two contractile vacuoles, and an eye-spot, so that in all essential respects it resembles a naked *Carteria*.

The pear-shaped motile elements thus formed are the asexual reproductive cells or *zoospores* (Fig. 194, D), which can swim after the manner of a *Chlamydomonas* for several hours, and thus travel some distance away from the parent filament. During most of this time they seek out well-lighted regions of the water, but ultimately they tend to move towards darker spots, where they usually come to rest on the surface of stones. The zoospore flattens out against the substratum and the flagella are withdrawn (Fig. 194, E, F); a cell-

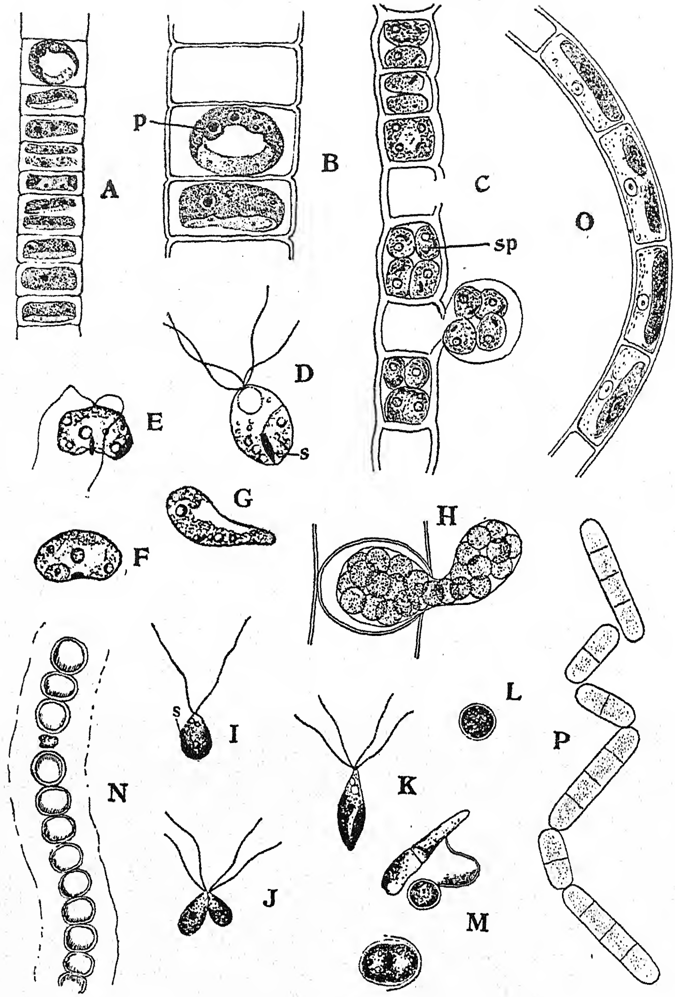


FIG. 194. A–N, Structure and reproduction of *Ulothrix*. A, B, Parts of threads to show structure of chloroplast, etc. C, Thread showing stages in the development of zoospores (*sp*). D, Zoospore. E, The same coming to rest. F, G, Stages in its germination. H, Liberation of gametes. I, Gamete. J, Fusion of gametes. K, The resulting zygote. L, Zygospore. M, Germination of same. N, Formation of resting spores. O, P, *Hormidium*. O, Vegetative thread. P, Fragmentation. *p*, pyrenoid; *s*, eye-spot. (A, B, N, after Fritsch; D–G, after Gross; H, after West; the rest after Klebs.)

wall is secreted (Fig. 194 F) and then, by gradual elongation and division, there is produced a new filament (Fig. 194, G), which soon breaks away from its attachment and becomes free-floating. Such asexual reproduction is obviously very prolific.

The *gametes* are formed and liberated in exactly the same way as the zoospores, except that 16 or even 32 may be formed in a cell (Fig. 194, H). The isogamous sexual cells (I), which differ from the zoospores only in their small size and in having but two flagella, behave just as in *Chlamydomonas*, those from different filaments fusing together in pairs (J) to form a quadriflagellate zygote (K) which, soon after, comes to rest and secrets a thick wall (L). The resulting zygospore remains in a dormant condition during the hot season, and may be dispersed in the same way as in *Chlamydomonas* (cf. p. 276). On germination, the contents divide usually into four parts, each of which gives rise to a new thread (Fig. 194, M). During the greater part of its life-history *Ulothrix* is thus sedentary, but motility is associated with reproduction. A form is then assumed resembling that of the unicellular organisms which are motile throughout their existence.

At certain times the cells of the ordinary *Ulothrix*-threads, after thickening their walls and becoming laden with food-reserves, often fall apart and form as many separate resting spores (Fig. 194, N).

The reproductive cells of *Cladophora* are essentially similar to those of *Ulothrix*, but in several species the zoospores and gametes are produced in distinct plants and both are, moreover, formed in large numbers (Fig. 183, C); the cells developing them are usually restricted to the finer branches. During periods that are unfavourable to vegetative growth (*e.g.* the cold months of the winter), many of the finer branches are shed and the remaining cells become laden with food-reserves and develop thicker walls.

All the higher Algæ resemble *Ulothrix* and *Cladophora* in the restriction of motility to the reproductive phase, which, however, exhibits a varying degree of specialisation. Vegetative propagation by *fragmentation* (*i.e.* cell-separation without preparatory division) is common, as in *Spirogyra*. In *Hormidium*, an alga common on damp soil, this is the customary method of propagation during a great part of the year (Fig. 194, P). The thick-walled threads of *Cladophora* just mentioned often fragment in a similar manner, before renewed growth takes place. Formation of new individuals by cell-division is the commonest form of reproduction in Desmids and Diatoms, whilst the filamentous members of the Blue-green Algæ propagate abundantly by mere fragmentation. In such massive forms as *Fucus*, the same end is attained by the detachment of small adventitious branches of the thallus, which are often formed

in bunches from the midrib and stalk, and are especially characteristic of the unattached species of this genus which occur on salt-marshes.

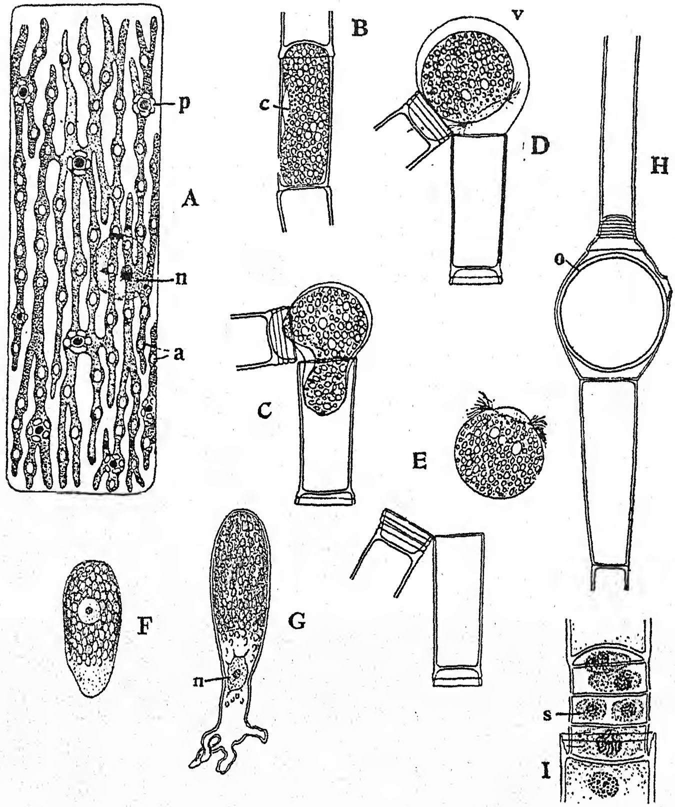


FIG. 195. *Œdogonium.* A, Single cell, highly magnified (after Schmitz), showing the net-like chloroplast with starch-grains (*a*), pyrenoids (*p*), and the single nucleus (*n*). B–G, *Œdogonium concatenatum* (after Hirn). B–D, Stages in formation of zoospores. E, Liberation of ditto. F and G, Germination of zoospores (in G the characteristic attaching cell is seen). H, *O. lautumniarium* (after West), showing an oogonium (*o*), with caps. I, *O. Boscii* (after Hirn), antheridia, with young spermatozoids. *c*, front end of future zoospore; *n*, nucleus; *s*, spermatozoid; *v*, vesicle.

Many Green Algæ reproduce asexually by means of *zoospores*, but these often possess a more elaborate structure than those of *Ulothrix*. For example, in *Œdogonium*, where they are produced singly from the ordinary cells, they are much larger and bear a ring of flagella a little way behind the colourless front end

(Fig. 195, E). If filaments of this Alga are grown in water indoors, zoospores are usually formed within a few hours, and their development and liberation can be observed more readily than in other fresh-water Algæ.

The protoplast contracts slightly away from the wall, and a colourless area, marking the future front end of the zoospore, arises on one side (Fig. 195, B); the nucleus moves towards this side of the cell (cf. p. 40). Around the edge of the colourless area the numerous short flagella sprout out, appearing as fine lines. Thereupon the wall breaks across, near one end of the cell, and the shorter piece hinges back to form an aperture through which the contents slowly glide (C). When liberated the almost spherical zoospore is surrounded by a thin bladder of extruded mucilage (D), but it almost immediately commences to move away (E) with the help of its flagella. Sooner or later the zoospore becomes

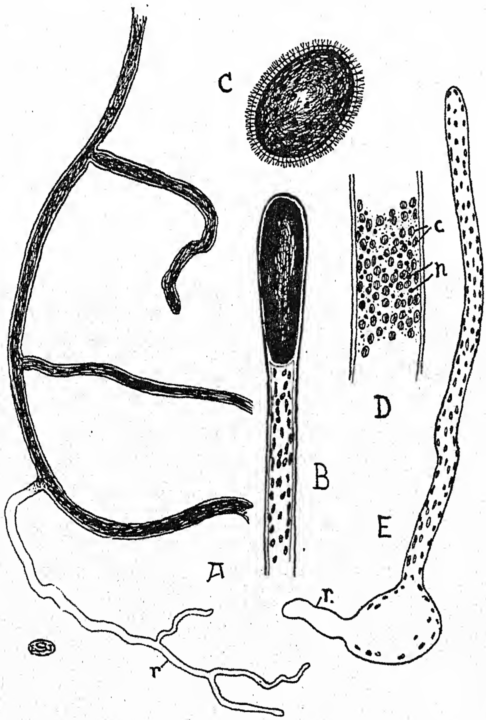


FIG. 196. *Vaucheria*. A, Portion of a plant showing the branched non-septate thallus and the colourless rhizoid-like attaching organ (*r.*). B, Zoosporangium. C, Zoospore. D, Small part of thallus, showing the numerous chloroplasts (*c*), and nuclei (*n*). E, Germinated zoospore. (C after Oltmanns; rest original.)

attached to some submerged object by its colourless front end (Fig. 195, F), and the flagella are withdrawn; then a cell-wall is secreted and division takes place to form a new filament, whilst the end in contact with the substratum grows out into the branched holdfast (Fig. 195, G).

In *Vaucheria*, zoospore-production involves swelling of the tips of the branches, which become cut off by a wall to form a *zoosporangium* (Fig. 196, B). Within this the contents round off and the numerous nuclei take up a peripheral position. A pair of flagella arise opposite each nucleus, and the large multi-flagellate oval zoospore (Fig. 196, C) escapes into the water by the breaking down of the tip of the thread. After a short period of movement a thin wall is formed and the two ends lengthen into tubes, of which one frequently penetrates the soil or mud and becomes a colourless attaching organ (Fig. 196, E, *r*.).

Zoospores are also found in various Brown Algæ, *e.g.* in *Ectocarpus*, *Chorda*, and *Laminaria.* In the first-named they develop in sporangia of two kinds, each borne laterally on a branch of the filament (Fig. 197, B). The one kind (unilocular, Fig. 197, B and H, *u*) produces several zoospores which are liberated by rupture of the apex. The other kind (plurilocular, Fig. 197, B, C, *p*) are divided by horizontal and vertical walls, each of the numerous small compartments producing one zoospore. In *Laminaria* and *Chorda* dense patches of unilocular sporangia, interspersed with protective unicellular outgrowths (paraphyses) (Fig. 198, A, B, *u*) occur as darker areas on the fronds. The pear-shaped zoospores (Fig. 197, D; Fig. 198, C) have two flagella, one directed forwards and the other backwards during movement, and these are attached to one side adjacent to the chloroplast (*c*) and the prominent eye-spot (*s*).

The production of zoospores serves as a rapid means of multiplication and dispersal at times when vegetative activity is at its height, but this method lacks the stimulus which sexual fusion appears to provide. There are quite a number of Algæ in which a *sexual process* is unknown, as in the whole group of the Cyanophyceæ and in many Desmids. Apart from these, however, most Algæ reproduce sexually at some time or other. In many freshwater Algæ sexual fusion results, as in *Ulothrix,* in the production of resistant spores and, in contrast to the asexual method, is frequently associated with the onset of conditions adverse to the plant's growth.

The fusing gametes are outwardly alike in *Ulothrix* and *Cladophora,* as well as in most species of *Chlamydomonas*, excepting *C. braunii.* The dissimilarity in size and behaviour of the sexual

cells seen in this species (cf. p. 275) is paralleled, or even more emphasised, in the higher Algæ. A relatively simple instance is afforded by *Ectocarpus*, where the gametes are produced in elongate

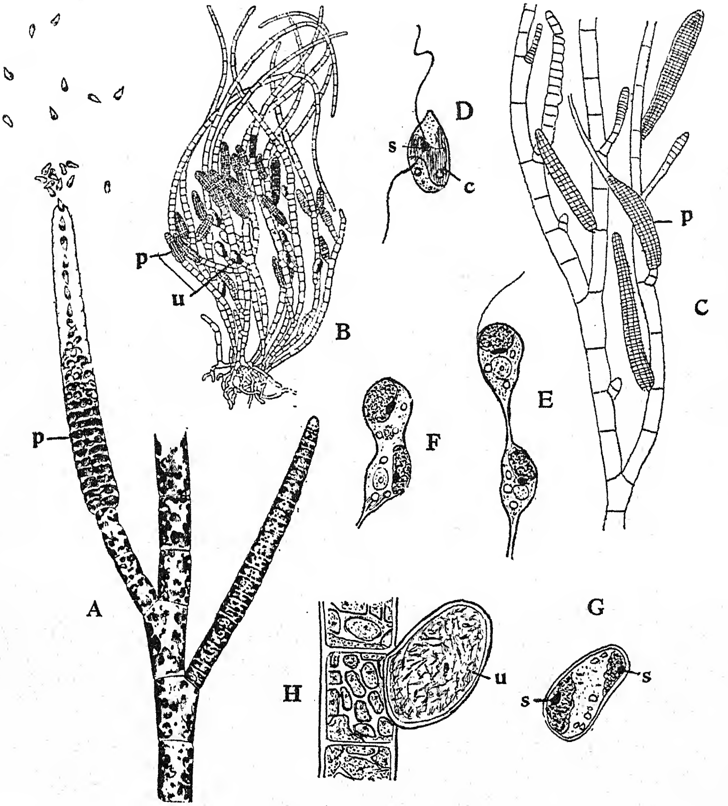


FIG. 197. Structure and reproduction of *Ectocarpus*. A, Small part of a thread showing a gametangium (*p*) liberating gametes. B, Diploid plant showing creeping and erect threads, the latter bearing unilocular (*u*) and plurilocular (*p*) sporangia. C, Branched haploid filament with several gametangia (*p*). D, Zoospore: *c*, chloroplast; *s*, eye-spot. E, F, Stages in fusion of gametes. G, Zygote, with two chloroplasts and two eye-spots (*s*). H, Small part of thread with a unilocular sporangium (*u*). (A, after Thuret; B, after Setchell and Gardner; C, after Migula; D and H, after Reinke; E–G, after Berthold.)

gametangia (Fig. 197, A, C), similar in position and form to the plurilocular sporangia above described and only to be distinguished by the behaviour of the contents. Each compartment forms a single gamete (Fig. 197, A). These sexual cells are smaller, but otherwise resemble the zoospores. Despite their structural uni-

formity, some gametes are relatively sluggish, and, after a brief period of movement, become attached to any suitable substratum by a disc-like expansion at the end of their forward flagellum, whilst others move actively and for a much longer time. The latter ultimately collect in groups around the others and, sooner

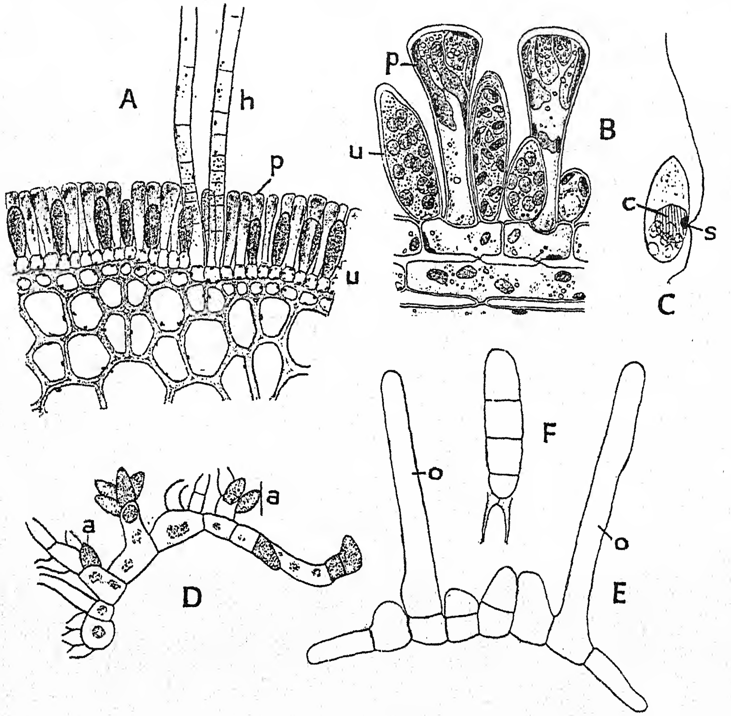


FIG. 198. Reproduction of Laminariaceæ. A, Section of series of unilocular sporangia of *Chorda*, and B, small part enlarged (both after Reinke). C, Zoospore (after Sauvageau). D, Male, and E, female gametophytes (after Printz and Sauvageau). F, Germling from fertilised ovum. *a*, antheridia; *c*, chloroplast; *h*, hair; *o*, oogonium; *p*, paraphyses; *s*, eye-spot; *u*, unilocular sporangia.

or later, an active gamete fuses with a resting one (Fig. 197, E and F). There is thus a marked difference in behaviour between the two fusing cells, but the differentiation into active males and passive females is here purely physiological.

The distinction between the two sexes is much more marked in genera like *Œdogonium*, *Vaucheria*, and *Fucus*, where one sexual cell (the female or *egg*) is large, motionless, and provided with plentiful food-material, whilst the other (the male or *spermatozoid*)

is small, actively motile, and possessed of very scanty cytoplasm. The two kinds of gametes are usually formed in special sexual organs differentiated from ordinary vegetative cells; that producing the egg (*ovum*) is termed the *oogonium*, whilst that forming the spermatozoids is known as the *antheridium*.

In *Œdogonium* the oogonia are more or less oval cells which develop from cap-cells (p. 284) and occur either singly or in short chains (Fig. 195, H, *o*). At one point the wall of the oogonium develops a small papilla by the breaking down of whose tip an aperture for the entry of the male cells is created (Fig. 199, C); in some species of *Œdogonium*, however, opening is effected by a complete transverse split in the wall. The single egg, formed by the contracted protoplast of the oogonium, develops a small colourless area, adjacent to the aperture, known as the *receptive* spot (Fig. 199, C, *r*), and at this point a quantity of mucilage is extruded shortly before fertilisation.

The antheridia are small and tabular, being formed by repeated transverse division of cells of the filament (Fig. 195, I). Each antheridium produces two spermatozoids (*s*) which are diminutive, yellowish-green replicas of the zoospores, liberated in the same manner.

Spermatozoids are attracted to the oogonia, probably by some chemical substance [1] in the extruded mucilage, and, passing through the aperture, penetrate into the egg, the cytoplasm and nucleus of the one thereupon fusing with those of the other. Neither sexual cell can develop independently.

It is customary to speak of such sexual union as *fertilisation*. The effects of the fusion are probably always essential to further development, and the stimulus provided is doubtless both chemical and physical in character. This view is supported by the fact that eggs of Sea-urchins have been induced to develop into embryos by mere immersion in suitable solutions, whilst those of the Frog have been caused to undergo the first stages of development by mere pricking. Moreover, in plants, fertilisation sometimes stimulates other cells near the egg to develop into embryos (cf. p. 473).

The fertilised eggs, or *oospores*, of *Œdogonium* develop thick protective walls and fatty pigmented contents and, as the filaments containing them die away, sink to the bottom of the water. Here they pass through a prolonged resting period, and, should the pond dry up, may be dispersed by the wind. In germination they

[1] The influence exerted by chemical substances on the direction of movement of motile elements is spoken of as *chemotaxis*, and the positive chemotaxis evident in sexual union is only one of many examples of such chemical stimulation (cf. p. 318).

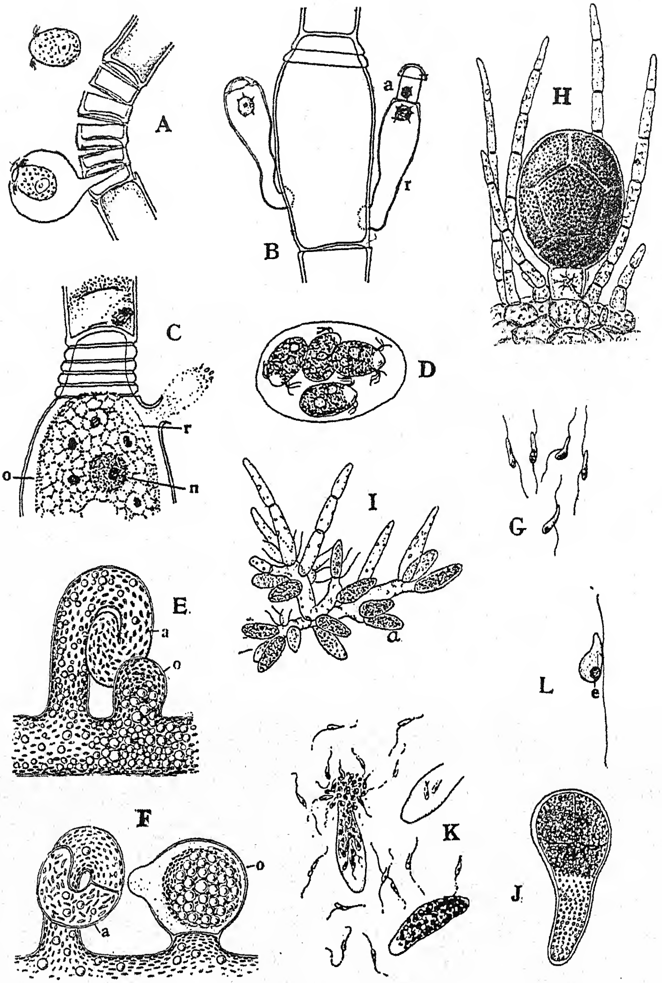


FIG. 199. Oogamous sexual reproduction among the Algæ. A–D, *Œdogonium*. A, Part of thread of *O. braunii*, showing liberation of special zoospores that form the dwarf-males. B, Oogonium of *O. concatenatum*, with two dwarf-males. C, Apical part of oogonium of *O. boscii* showing the receptive spot (*r*). D, Germinating zygote showing the four zoospores. E–G, *Vaucheria sessilis*. E, Young oogonium (*o*) and antheridium (*a*). F, The same almost mature. G, Spermatozoids. H–L, *Fucus*. H, Oogonium, with surrounding hairs. I, Branched hair bearing numerous antheridia (*a*). J, Young plant. K, Liberation of spermatozoids. L, Spermatozoid. *a*, antheridium; *n*, nucleus; *r* (in B), rhizoid of dwarf-male. (A, B, after Hirn; C, after Klebahn; D, after Juranyi; E, F, after Oltmanns; G, after Woronin; H–K, after Thuret; L, after Guignard.)

usually give rise to three or four zoospores (Fig. 199, D), which are set free by the bursting of the thick membrane.

The sexual organs are arranged in various ways in the different species of *Œdogonium*, male and female sometimes occurring in the same filament (monœcious forms), sometimes in different filaments (diœcious forms); in the latter the male plants often consist of only a few cells (*dwarf males*, Fig. 199, B), and arise from special smaller zoospores (Fig. 199, A) which become attached to the female plant, on or near an oogonium.

It will be evident that *Œdogonium* exhibits considerable specialisation in its methods of multiplication, and not the least conspicuous feature is the division of labour manifest in the *oogamous sexual reproduction*. Owing to its stationary character, the egg can possess the greater bulk which a more adequate provision of food-material for the benefit of the next generation necessarily entails (cf. p. 306). Since the spermatozoids contribute nothing to this food-supply, they can be correspondingly smaller, and therefore, without additional strain on the organism, produced in larger numbers, whereby the chance of fertilisation occurring is greatly increased. The probability of fusion between the two gametes is, moreover, doubled by one of them remaining stationary. The greater certainty of sexual union admits of a corresponding decrease in the production of eggs, which will afford as many off-spring as would a larger number of motile female gametes. These remarks apply with equal force to all plants in which oogamy occurs.

The oogonia and antheridia of *Vaucheria* are produced near one another as outgrowths (Fig. 199, E) of the main filament or of short lateral branches, from which in either case they become cut off by a septum (Fig. 199, F). Their relative positions are very diverse, but the adjacent sexual organs usually mature almost simultaneously, so that self-fertilisation is probably the rule. The more or less oval oogonium (*o*) develops a protrusion on one side, whose tip becomes mucilaginous, and breaks down to form the aperture through which the male cell enters. The mature egg possesses a pronounced receptive spot and contains only a single large nucleus.

The antheridium is a coiled tube (Fig. 199, F, *a*) and gives rise to numerous minute pear-shaped spermatozoids with two laterally attached flagella (Fig. 199, G); they are liberated by breaking open of the tip of the antheridium. The attraction of the spermatozoid towards the egg is probably again connected with the extrusion of mucilaginous matter by the latter. After fusion, the oospore becomes enveloped by a thick wall and accumulates large stores of oil; it then enters on the usual resting period, which is ultimately terminated by the direct development of a new plant.

Apart from the vegetative propagation above described, *Fucus* exhibits only sexual reproduction, the antheridia and oogonia being developed in the large *fertile conceptacles* occupying the swollen tips of the thallus (Fig. 187). In some species (e.g. *F. spiralis*) the two kinds of sexual organs occur in the same conceptacle, but in *F. vesiculosus* and *F. serratus* there are distinct male and female plants. The globular cavities of the conceptacles (Fig. 200, A) are separated from the interior of the thallus by a wall (*w*) composed

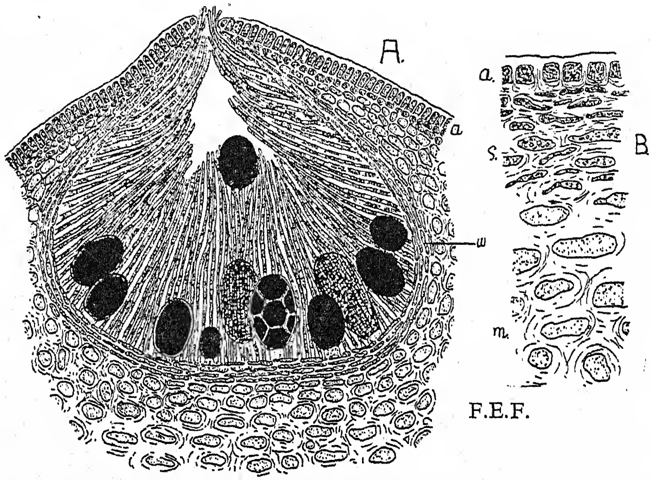


Fig. 200. The Bladder Wrack (*Fucus vesiculosus*). A, Vertical section through a fertile conceptacle, containing oogonia in different stages of development. B, Small part of a transverse section through the thallus, more highly magnified. *a.*, photosynthetic layer; *m.*, medulla; *s.*, storage cells; *w.*, wall of conceptacle.

of several layers of flattened cells, from whose inner surface arise numerous multicellular hairs bending towards, and some often protruding from, the small aperture; in the fertile conceptacles the sexual organs are interspersed among these hairs (Fig. 200, A).

The oval oogonia possess a thick transparent several-layered membrane, and are seated on a unicellular stalk which arises directly from the wall of the conceptacle (Fig. 199, H; 200, A). At maturity the contents are divided into eight uninucleate eggs, containing abundant chloroplasts and separated by delicate walls. The antheridia are oval cells, which likewise possess relatively thick walls and occupy the ends of most of the short lower segments of richly branched hairs (Fig. 199, I).[1] In each are formed

[1] These antheridial hairs are best examined by teasing out the contents of a male conceptacle in a drop of water.

numerous minute biflagellate spermatozoids (Fig. 199, L), containing a well-marked nucleus, but only traces of a chloroplast. The mature antheridia have a yellowish colour, which they impart to the entire conceptacle, and by this means, in the diœcious species, the male plants can be distinguished.

When the sexual cells are ripe, the outermost layer of the antheridium or oogonium breaks open and sets free the contents enclosed in the inner part of the wall. The gradual extrusion of the packets of ova, or spermatozoids, from the opening of the conceptacle often occurs between the tides, and is probably largely brought about by expansion of the mucilage, secreted by the hairs, combined with desiccation and contraction. The sea-water dissolves the membranes still enveloping the sexual cells (Fig. 199, K), and the ova, which have now assumed a spherical form, become fertilised by the actively moving spermatozoids. The oospore secretes a thin membrane and immediately, without a resting period, develops into a new *Fucus*-thallus. The young plant is at first spherical, but at an early stage produces the basal holdfast (Fig. 199, J) and acquires a strap-shaped form, and this is soon followed by branching.

In *Pelvetia*, where both sexual organs occur in the same conceptacle, the oogonium has an exceptionally thick wall and produces only two eggs. Extrusion of the sexual cells takes place in the same way as in *Fucus*.

Fucus and *Pelvetia* differ from most other oogamous plants in the number of eggs and in the fact that the latter are fertilised outside the plant, in both of which respects these Algæ appear relatively unspecialised. Normally the female organ contains but a single ovum (cf. *Œdogonium*, and the higher plants), and in this connection it is interesting to note the reduction of the eggs to two in *Pelvetia*, though here also the nucleus divides into eight parts, six of which abort.

The Conjugatæ (cf. p. 296) owe their name to a very special type of sexual reproduction (*conjugation*), in which neither gamete is free-swimming. In the filamentous forms, such as *Spirogyra* and *Zygnema*, two threads come in contact with one another, and their opposing cells develop finger-like protrusions, which, as they lengthen, push the threads apart (Fig. 201, B); after this the separating wall breaks down, so that an open tube (the conjugation canal, Fig. 201, *c.c.*) is established. In *Spirogyra* and many species of *Zygnema* the development of processes always commences a little sooner on the one filament than on the other, and a similar difference is observed with respect to the contraction of the protoplasts which now ensues. The cells of the filament that first put

out processes act as males, since their contents commence to glide over, through the conjugation canals, into the opposite cells (Fig. 201, B, *b*), with whose passive (female) protoplasts they fuse.

In some species of *Zygnema* (e.g. *Z. pectinatum*), however, the events leading up to conjugation take place simultaneously in the two filaments, and the fusing protoplasts contract to the middle of the conjugation canal; in such forms there is no outward

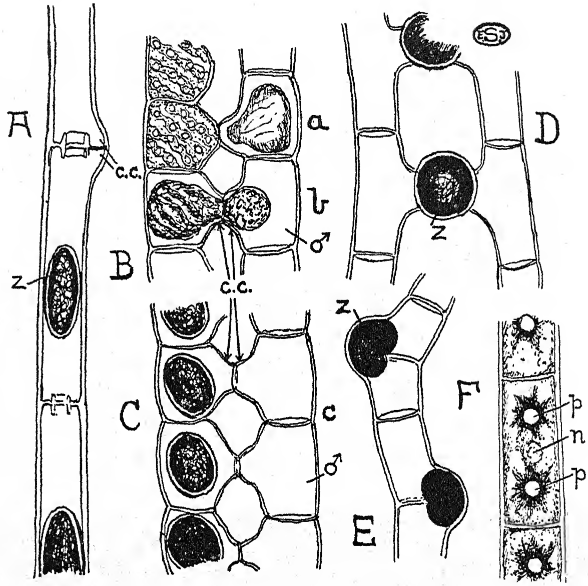


FIG. 201. Sexual reproduction in various Conjugatæ. A, *Spirogyra weberi*, showing lateral conjugation (after Petit). B and C, *Spirogyra bellis*. B, Successive stages (*a* and *b*) in conjugation; C, completed conjugation. D, Ladder-like, and E, lateral conjugation in *Zygnema pectinatum*. F, Small part of filament of same. *c.c.*, conjugation canal; *n*, nucleus; *p*, pyrenoid; *z*, zygospore; ♂ =male cells

differentiation of sex, the gametes being isogamous as in *Ulothrix* (Fig. 201, D). But even in *Spirogyra* the gametes are essentially distinguished physiologically.

In some species, both of *Spirogyra* and *Zygnema*, sexual union may take place between adjacent cells of the same filament (Fig. 201, A and E), the conjugation canals (*c.c.*) forming loop-like connections between their contiguous ends. Here the threads must be regarded as including cells of both sexes, the zygospores as before being formed either in the conjugation canal or in one of the two cells. The fact that both methods of conjugation may

occur simultaneously in the same weft of *Spirogyra* or *Zygnema* indicates that sexual differentiation between the filaments is not very profound.

The zygospores (Fig. 201, *z*) always secrete a thick several-layered wall and pass through a prolonged resting period, during which they may be distributed in the customary manner by the wind. On germination the membrane bursts, the contents growing out to produce a new filament, one end of which may form an attaching cell.

Among the Desmids where sexual reproduction is rare, fusion takes place between the liberated protoplasts of two individuals, which usually become enveloped in mucilage. The empty halves of their cell-walls are often recognisable near the resulting zygospores (Fig. 193, I), which frequently have elaborately sculptured membranes. In some of the Diatoms a sexual process of an analogous type is encountered.

The Red Algæ possess only motionless reproductive cells, and exhibit a very complex sexual process whose description is beyond the scope of this book. There is, however, a copious production of filamentous outgrowths from the female organ after fertilisation, the ends of these threads giving rise to special asexual reproductive cells known as *carpospores*. The dense clusters thus produced are often conspicuous as minute patches of a darker colour. The ordinary asexual cells, so-called *tetraspores* (Fig. 190, A) are produced in fours in small usually spherical sporangia on other plants.

The examples of reproductive processes among the Algæ might be multiplied considerably, but sufficient have been described to show the diversity of methods by which the same end, namely, the multiplication and perpetuation of the species, is attained. It is the result rather than the means which must be regarded as the more important biological phenomenon, indeed in the less specialised Algæ several different means of attaining this end may occur. With all the variety in reproductive methods, the outcome is a cell, or cells, each capable of giving rise to a new plant.

The product of sexual fusion is often a comparatively large spore well supplied with food-material for the next generation. It is, however, easy to recognise the importance of a second type of multiplication, by zoospores which, being unprovided with either food-reserves or resistant walls, can be formed rapidly and in large numbers, thus giving great facility of responding to favourable conditions.

During nuclear division the chromatin has been seen to take the form of definite chromosomes whose number is constant for one kind of plant (p. 55). When two gametes fuse the resulting

nucleus contains twice the normal number of chromosomes, *i.e.* is diploid. Sooner or later, however, division of a special type occurs (reduction division, see p. 590) during which entire chromosomes pass to the daughter nuclei so that the normal (haploid) condition is again restored. In many of the simpler Algæ (*Ulothrix*, *Œdogonium*) in which the zygote divides to form zoospores (Fig. 199, D), or other asexual cells, the first nuclear division is the reduction division and restores the haploid number; the zygote is therefore the only diploid phase in the life-cycle. In some species of *Cladophora*, however, the zygote grows direct into a diploid asexual plant, reproducing by zoospores only, identical externally with the haploid gamete-bearing plant. Here the asexual and sexual phases alternate.

In *Ectocarpus* the diploid asexual and the haploid sexual individuals are likewise usually similar. It is in the unilocular sporangium (Fig. 197, H) of the diploid individual that reduction in chromosome number occurs so that the resulting swarmers are haploid, whilst the zoospores from the plurilocular sporangia remain diploid and serve to propagate the diploid plant.

The haploid zoospores give rise to sexual individuals, but these too can often propagate indefinitely by means of gametes which germinate without fusion, thus behaving like haploid zoospores. The zygote, on the other hand, grows into the diploid plant. In northern latitudes diploid individuals propagating solely by asexual means may occur, a phenomenon paralleled in some Flowering Plants. A comparable alternation is shown by most Red Algæ in which tetraspores and carpospores are formed on distinct though otherwise similar plants. In all these alternations the change from the diploid to the haploid number of chromosomes occurs when the zoospores (or tetraspores) are formed.

Markedly dissimilar generations are found in *Laminaria* and its allies, in which the large diploid thallus reproduces only by haploid zoospores, which give rise to minute haploid *Ectocarpus*-like filaments producing either antheridia (Fig. 198, D) or oogonia (Fig. 198, E). The spermatozoids fuse with the ova and the zygote develops at once into the asexual plant. This type of alternation is of special interest because it closely parallels the condition in Mosses and Ferns (cf. p. 368).

[For a more detailed treatment of the Algæ, see F. E. Fritsch, *The Structure and Reproduction of the Algæ*, Cambridge University Press, 1935 (791 pp.), a comprehensive account of algal morphology; and F. Oltmanns, *Morphologie und Biologie der Algen*, 3 vols., Gustav Fischer, Jena, which includes also many biological data. A useful reference work is: H. B. Ward and G. C. Whipple, *Freshwater Biology*, Wiley & Sons, New York, 1918 (1111 pp.). For taxonomic works, see p. 579.]

CHAPTER XXVIII

THE STRUCTURE AND REPRODUCTION OF THE FUNGI

THE *Thallophyta*, the first class of the Vegetable Kingdom, include not only the chlorophyll-containing Algæ, but also the Fungi[1] which contain no chlorophyll. These are, consequently, like the colourless saprophytes and parasites among higher plants, dependent upon organic material elaborated by other organisms.

A considerable number derive all their nourishment from other *living* plants or animals, such *parasites*, exemplified by the Smut of Wheat, the Gooseberry Mildew, the Potato Blight, the Salmon and Silkworm diseases, often doing serious harm to their hosts. Numerous Fungi, however, live upon decaying organic matter (*e.g.* many Moulds and Toadstools), and these *saprophytes* play an important part in nature in connection with processes of decay and the circulation of nutritive materials.

Fungi show many peculiarities, both in vegetative structure and the nature of their reproductive processes. The plant-body is of a peculiar type, consisting generally of a loose weft, the *mycelium* (Fig. 204, *a*), composed of very delicate branched threads or *hyphæ*, which may or may not be septate (Fig. 208, *a*). The narrow diameter of the hyphæ facilitates their penetration either into the interior of a host (parasites), or between the particles of decaying organic material (saprophytes). The hyphæ, moreover, secrete at their tips various enzymes (cf. p. 83), which bring about solution of the obstructing cell-walls and also convert the organic material into a readily assimilated form, a single species of Fungus producing a number of different enzymes, according to the substratum upon which it occurs. The extreme simplicity of the vegetative structure may well be compared with that of parasitic Flowering Plants, some of which have a plant-body so reduced that it resembles a mycelium (cf. p. 215).

In some Fungi the wall of the hyphæ consists of cellulose, but much more commonly of a complex nitrogenous compound

[1] For reference-books, see p. 334.

similar to the chitin found in animals, together with other substances such as pectose, callose, etc. Embedded in the lining layer of cytoplasm in the lower forms are numerous minute nuclei, but in the septate hyphæ of the higher types there are usually only one or two in each cell; neither plastids nor starch-grains are ever present, but there are often small oil-drops and sometimes crystalline albuminous bodies. The central vacuole is prominently developed. Where abundant food-storage occurs, as, for instance, in the reproductive cells, it is customary to find the polysaccharide *glycogen*, which assumes a brown colouration with iodine. In coloured hyphæ, such as occur in species of *Peziza*, etc., the pigment is either located in the cell-wall or in granules.

The Fungi are classed in three main groups—Phycomycetes, Ascomycetes, and Basidiomycetes—each of which has many characteristic features. The *Phycomycetes*, which are not modified to so marked an extent as the other two groups, include forms which usually show a well-marked sexual process, and which, in this and other respects, resemble Algæ such as *Vaucheria*. The hyphæ, for example, contain numerous nuclei, and often only exhibit transverse walls in relation to the formation of reproductive bodies. The group includes many common parasites, such as *Cystopus* (the White Rust of Cruciferæ, Fig. 202, A), *Pythium debaryanum* (the cause of the "damping off" of seedlings, Fig. 203, B), *Phytophthora infestans* (the Potato Blight), *Empusa* (responsible for a disease of house-flies), as well as the saprophytes *Mucor* (the black Mould appearing on jam, bread, etc.), *Saprolegnia*, and *Achlya* (the last two frequent on decaying water-plants).

Cystopus, a species of which often attacks the Shepherd's Purse, furnishes a typical example, whose life-history can easily be studied. The parts affected by the Fungus are swollen and contorted (Fig. 202, A), and exhibit a white surface. Such enlargement, or *hypertrophy*, is a frequent symptom of fungal attack, and is an outcome of the abnormal development of the diseased tissue, whose cells undergo increase in size with, or without, division. A longitudinal section through such a swelling (best stained with eosin) shows the hyphæ within the intercellular spaces and middle lamellæ of the host. Here and there larger hyphæ (Fig. 202, B, *h*) bearing small club-shaped branchlets (the *haustoria*, *S.*), and belonging to another Fungus (*Peronospora parasitica*), commonly associated with *Cystopus*, will be observed in the actual cell-cavities. By similar but finer hyphæ *Cystopus* absorbs food-material elaborated by the host.

Near the surface of the stem the hyphæ are more densely packed, and their almost parallel branches form a pile-like felt (the *hymenium*, Fig. 202, C) which ruptures the overlying epidermis and causes the

white appearance above mentioned. The slightly swollen ends of the hyphæ of the hymenium exhibit various stages of constriction,

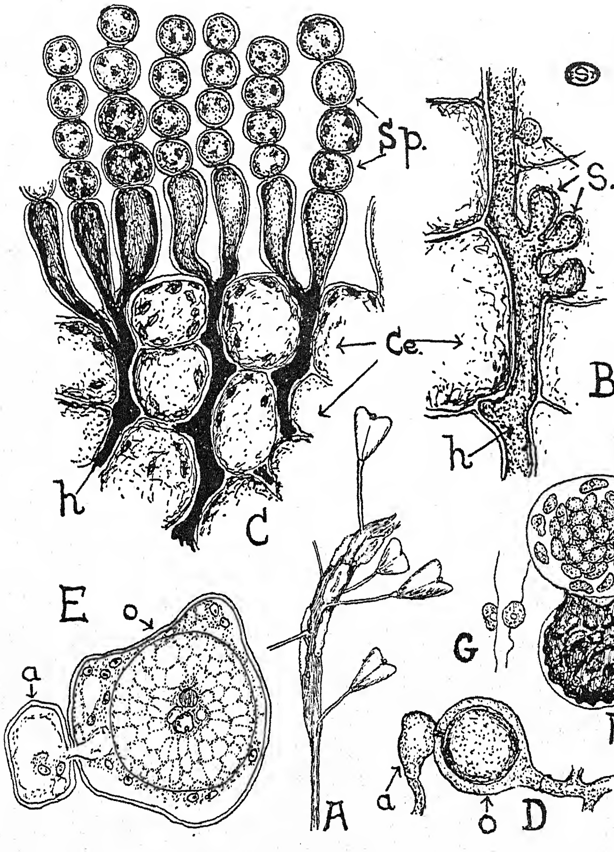


FIG. 202. The White Rust of Cruciferæ (*Cystopus candidus*). A, Diseased inflorescence of Shepherd's Purse, showing the white patches where the conidia of the Fungus are being formed. B, Hypha (*h*) of *Peronospora*, with haustoria (*S*.), in a longitudinal section between the cells (*Ce*.) of the host. C, Transverse section near surface of host, showing hyphæ (*h*) and conidia (*Sp*.). D, Antheridium (*a*) and oogonium (*o*) (after De Bary). E, The same in section at the time of fertilisation (after Stevens). F, Germination of oospore (after De Bary). G, Zoospores (after De Bary). All, except B, of *Cystopus*. (Figs. A–C, original.)

resulting in the gradual formation of chains of spherical structures called *conidia* (*Sp*.), the oldest of which is farthest away from the point of origin. As the short fragile stalks connecting the conidia

with one another get broken across, the latter are removed by the wind, often to considerable distances.

When rain or heavy dew causes a sufficient accumulation of moisture, the contents of the conidia divide into several parts, which are liberated as minute colourless *zoospores* (Fig. 202, G), swimming by means of a pair of flagella. Many doubtless perish before reaching a suitable host, but should they encounter seedlings of a Cruciferous plant, they come to rest on the surface, secrete a membrane, and elongate into a short hypha which penetrates into the interior by way of a stoma. The stimulus directing the movement of the zoospore towards the host-plant is probably a chemotactic one (p. 307), whilst the growth of the hypha into the interior affords an example of positive chemotropism. For some weeks further development of the Fungus consists in the ramification and gradual spread of the hyphæ through the tissues of the host, until a sufficiently large haustorial system has been created to supply the material necessary for the production of conidia.

Sexual reproductive organs are usually produced towards the end of the host's flowering period (*i.e.* when the supply of nutriment probably becomes deficient), and arise in the interior of the infected regions. They consist of spherical *oogonia* (Fig. 202, D, *o*), generally situated at the ends of the same hyphæ as bear the club-shaped *antheridia* (*a*) at a slightly lower level. Both are multinucleate and, during development, undergo differentiation of their protoplasmic contents into a denser central and a less dense peripheral region (Fig. 202, E); the former constitutes the egg in the oogonium and the male gamete in the antheridium, while the outer region plays no part in sexual fusion.

The antheridium becomes applied to the female organ and puts out a slender tube which, piercing the oogonial wall, penetrates through the peripheral cytoplasm up to the egg (Fig. 202, D, E). The tip of the tube thereupon opens and the male gamete passes through it to fertilise the ovum, the process involving nuclear and cytoplasmic fusion in the usual way. The product becomes invested by a thick dark-coloured wall. After the decay of the host the *oospores*, which constitute the resting-stage in the life-history, may remain dormant in the soil for a considerable period. When conditions suitable for germination occur, the contents divide to form numerous zoospores (Fig. 202, F) which, after rupture of the thick wall, infect seedlings in the way already described.

Potato Blight and *Pythium debaryanum* have life-histories very similar to that of *Cystopus*, except that their conidia can, under certain circumstances, germinate direct into a new plant without forming zoospores. In both the mycelium is found within the host,

and the asexual reproductive organs alone appear on its surface. In the Potato Blight the oval or elliptical conidia are formed singly at the ends of branched hyphæ, which emerge through the stomata of the diseased leaves (Fig. 203, A). If blown on to the leaves of another Potato-plant, the conidia grow out direct

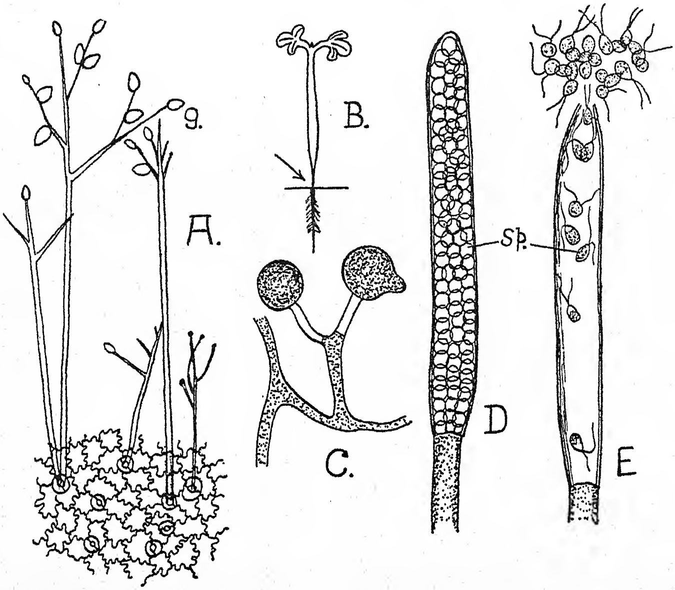


FIG. 203. Asexual reproduction in various Oomycetes. A, Small part of epidermis of Potato-leaf, infected with Blight (*Phytophthora infestans*), showing branched hyphæ bearing conidia (*g.*) emerging from the stomata. B, Seedling of Cress which is "damping off," due to an attack of *Pythium debaryanum*; where the hypocotyl is giving way is indicated by an arrow. C, Hypha with sporangia of the same. D, Young, and E older, sporangia of *Saprolegnia*, showing numerous zoospores (*Sp.*). (A, after Strasburger; B, after Miyake; C, after Hesse; D and E, after Thuret.)

into an infecting hypha; whilst, if they fall on the ground, they can, in the presence of moisture, produce zoospores, as in *Cystopus*. The first signs of disease are discoloured spots exhibiting a dark central region surrounded by successive zones of greyish and pale green tissue, which rapidly become brown or even blackish; closer inspection discloses the white tufts of hyphæ bearing the conidia, especially on the lower surface of the infected leaf. Infection of the tubers may be a result of downward spread of the hyphæ from the overground parts or by direct infection from conidia washed down by rain. Hence early removal of diseased shoots is advisable.

An attack of *Pythium* results in a rapid softening of the hypocotyls of the diseased seedlings (Fig. 203, B), which soon give way here and collapse. The rounded conidia, which are borne on simple or forked hyphæ (Fig. 203, C), usually give rise to zoospores without becoming detached, so that the disease rapidly spreads from one seedling to another. The sexual reproduction of *Pythium* and *Phytophthora* is practically identical with that of *Cystopus*.

Owing to the ease with which the Fungi just considered produce zoospores, which of course require a film of moisture in which to swim, spells of damp, warm weather are particularly favourable to their spread and development. Indeed, the damping-off of seedlings through attacks of *Pythium* only occurs in conditions of excessive humidity due to overwatering or overcrowding.

In the aquatic Phycomycetes reproduction by zoospores is the rule. The bacterial Salmon disease is usually accompanied by one of these Fungi (*Saprolegnia ferox*), which grows on the gills of the fish, where its wefts cause asphyxiation. The biflagellate zoospores are produced in large numbers in tubular sporangia (Fig. 203, D, E), whilst the only essential difference in the sexual reproduction of this genus lies in the development of several, or even many, eggs in each oogonium. In many of the species, moreover, the eggs develop into oospores without fertilisation (so-called apogamy), although functionless antheridia may be formed.

In contrasting the Fungi hitherto described with the Algæ, one of the most striking peculiarities, apart from the absence of chlorophyll, is the non-motile character of the male gamete. This feature may be related to the fact that the Fungi as a whole are a terrestrial group, living under conditions (*e.g.* in the interior of a host-plant) in which the necessary moisture for the movement of spermatozoids is not available.

The saprophytes among Phycomycetes are well exemplified by *Mucor*, which thrives on all kinds of decaying substrata (especially horse manure), upon which its mycelium forms a white weft (Fig. 204, *a*). Numerous absorptive branches penetrate downwards into the source of nourishment, and sooner or later conspicuous, dark brown or black, spherical *sporangia* (*sp.*) appear at the ends of relatively thick upright hyphæ, which in some species are branched. An ally of *Mucor* (*Rhizopus stolonifer*), that occurs very commonly on stale bread and horse dung, spreads very rapidly by hyphæ resembling minute strawberry runners, at the end of each of which a tuft of absorptive threads and sporangia is produced.

The wall of each sporangium (Fig. 204, *b*) is beset with numerous minute needles of oxalate of lime, whilst the swollen end of the hypha below projects into the cavity as a central column (*Co.*); between this and the wall are many small thick-walled spores embedded in a mucilaginous substance. The latter swells, in the presence of moisture, and thus contributes to the bursting of the

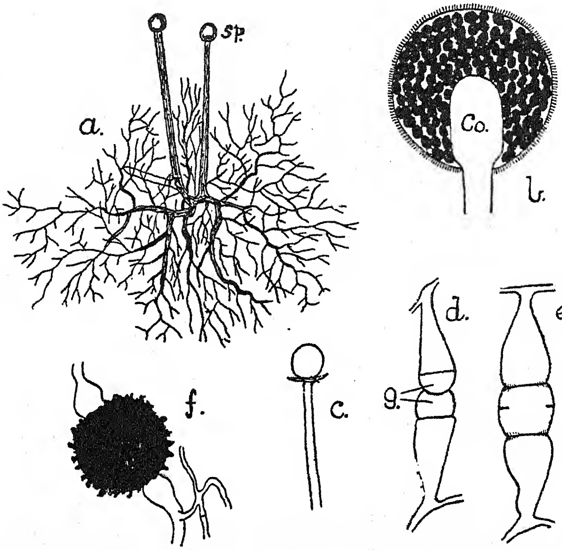


FIG. 204. *Mucor.* *a*, Mycelium, slightly magnified, showing two of the long-stalked sporangia (*sp.*); *b*, Sporangium, much enlarged, in optical section, showing the numerous spores and the central column (*Co.*); *c*, Dehisced sporangium in which only the column and a small part of the wall remains; *d* and *e*, Conjugation of gametes (*g.*); *f*, Mature zygospore. (*a*, *b* and *f*, after Brefeld; *c*, after Sachs; *d* and *e*, after De Bary.)

sporangium. It is also responsible for the adhesive nature of the spores, which are so widely disseminated by the wind that they are almost ubiquitous. They are extremely resistant, and are capable of remaining dormant for many years. On germination they grow direct into a new plant without the production of zoospores.

Sexual reproduction in most species only takes place between two mycelia belonging to physiologically distinct strains, not distinguishable outwardly (*heterothallism*). The gametes are produced within swollen club-shaped branches whose end-portions become separated off by cross-walls (Fig. 204, *d*, *g*.). Two perfectly similar branches meet by their tips, one being derived from each of the two plants (Fig. 204, *d*), and the intervening membrane

breaks down, whereupon fusion of the protoplasts and nuclei ensues (*e*). The product, deriving nutriment from the respective mycelia, subsequently undergoes slow enlargement to form a large spherical zygospore (Fig. 204, *f*). The latter on germination produces a short hypha terminating in a sporangium, some of the spores of which give rise to mycelia of the one and some to those

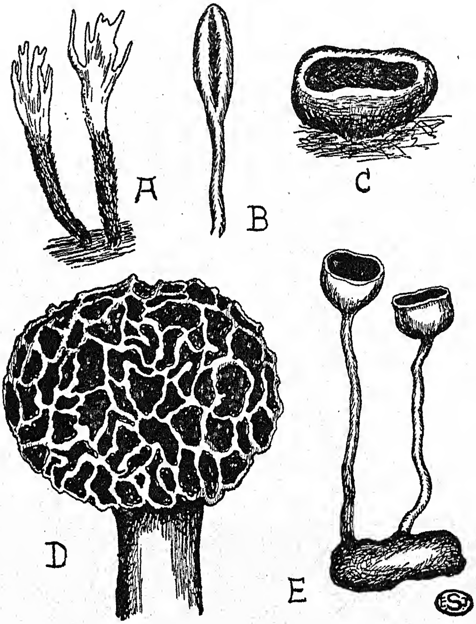


FIG. 205. Fruit-bodies of various Ascomycetes. A, *Xylaria hypoxylon* (Stag's Horn Fungus). B, *Geoglossum*. C, *Peziza* (Cup-fungus). D, *Morchella* (Morel). E, *Sclerotinia*, showing apothecia arising from sclerotium.

of the other strain. The sexual process of *Mucor* is thus isogamous and analogous to that of the Conjugatæ, where likewise an entire plant is often of one sex or the other (cf. p. 311).

Mucor and *Empusa* belong to a subdivision of the Phycomycetes, known as the *Zygomycetes*, all characterised by the possession of motionless spores and by the similarity of the fusing gametes. The other oogamous forms previously considered are classed as *Oomycetes*, but they are also distinguished by the ease with which they produce zoospores. The Zygomycetes are much more markedly adapted to terrestrial conditions from this point of view, since all of them reproduce by motionless spores.

The second main group of Fungi, the *Ascomycetes*, are characterised by their method of spore-formation and by the usual absence of a true sexual process. Common parasites belonging to this group are the Mildews (Erysiphaceæ), the Ergot of Rye (*Claviceps purpurea*, Fig. 207, A), and the Vegetable Caterpillar (*Cordyceps*); but there are numerous saprophytes, such as the ubiquitous Blue Mould (*Penicillium*), the Cup-fungi (species of *Peziza*, Fig. 205 C), the Stag's Horn Fungus (*Xylaria*, Fig. 205, A), the Morel

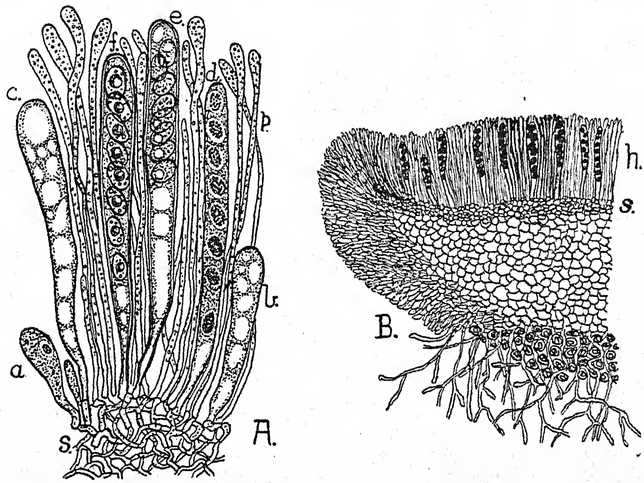


FIG. 206. *Peziza vesiculosa.* B, Section of half an apothecium (diagrammatic), and A, Small part of the hymenium enlarged, showing asci in progressive stages of development (*a–f*). *h.*, hymenium; *p.*, barren hyphæ of same; *s.*, small-celled subhymenium. (After Goebel.)

(*Morchella*, Fig. 205, D), and *Nectria*, which causes the bright red pustules common on decaying branches and sticks.

A general idea of the Ascomycetes can be obtained from an examination of *Peziza*. The septate mycelium of this Fungus is perennial and ramifies in the decaying substratum (*e.g.* dead trunks and branches, soil rich in humus), its presence only becoming apparent in autumn, when conspicuous, and often brightly coloured, cup-shaped fruit-bodies (*apothecia*, Fig. 205, C) are produced at the surface. In a vertical section through one of these (Fig. 206, B) the hyphæ are seen to be so densely compacted as to produce a *false tissue*, the elements of which are quite irregularly arranged, except for those lining the inner surface of the cup. These form a palisade-like layer (the *hymenium*, *h.*) composed of numerous elongated sporangia or *asci* (Fig. 206, A, *a–f*), interspersed with

the slender hair-like ends of barren hyphæ (*p.*). Each ascus contains eight ellipsoidal *ascospores* (*e*, *f*), which, on contact with moist air, are liberated when mature through a terminal aperture. Mere breathing on a ripe fruit-body may often cause the liberation of a cloud of spores.

The ascus is typical of the Ascomycetes as a whole, and constitutes one of their chief characteristics. For, by contrast with

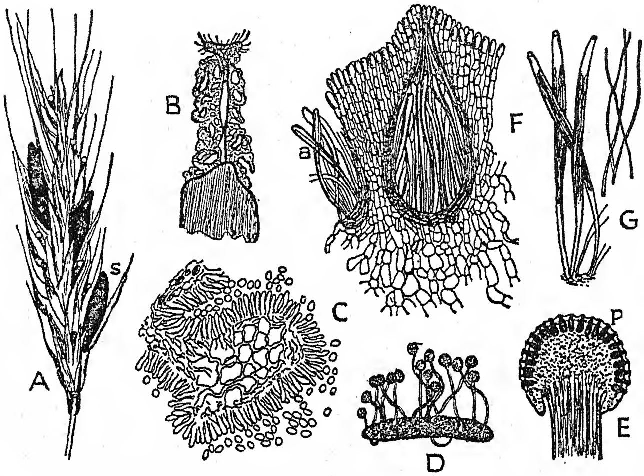


FIG. 207. Ergot of Rye (*Claviceps purpurea*). A, Head of Rye, with a number of black sclerotia (*s.*). B, Longitudinal section of ovary of Rye-flower, showing the dense hyphæ forming the sclerotium in the lower part, and the looser mass of hyphæ producing conidia in the upper. C, A small part of the latter in section, highly magnified, showing the budding off of conidia. D, Germinating sclerotium. E, Vertical section through one of the swellings arising from the latter, showing numerous perithecia (*p.*). F, Part of same, highly magnified, to show perithecia with asci (*a.*). G, Three asci and (on the right) four of the thread-like ascospores. (A and D, after Wettstein; the remainder after Tulasne.)

the Basidiomycetes (cf. p. 328), the spores are produced *within* the mother-cell, whilst in contradistinction to the Phycomycetes they are nearly always only eight in number. The asci, as in *Peziza*, are frequently grouped together in compact and large fruit-bodies, the hymenium either covering a great part of the exposed surface (as in *Morchella*, Fig. 205, D, and *Geoglossum*, Fig. 205, B) or being completely enveloped within sterile hyphæ, as in Truffles (*Tuber*), whose fruit-bodies are, moreover, subterranean.

Ergot (*Claviceps*) infests the ovaries of Rye, Oats, and other Grasses, becoming very conspicuous at the time of harvest, as a result of the gradual replacement of the grains by a black banana-

shaped mass (about half an inch long) of closely interwoven hyphæ (Fig. 207, A, *s.*). This constitutes a resting-stage of the Fungus, and is so hard that the term *sclerotium*[1] is applied to it. In transverse section all the hyphæ, and especially those at the periphery, are seen to have very thick walls, whilst the more central ones, forming the lighter-coloured region, are laden with food-reserves. The sclerotia drop off in the autumn and remain dormant in the soil until the following spring. Then they send up one or more stalked swellings (Fig. 207, D), in which are embedded numerous flask-shaped cavities (*perithecia*, Fig. 207, E, *p.*) communicating with the exterior by small pores (Fig. 207, F). Each perithecium is lined with a hymenium similar to that of *Peziza*, but the ascospores developed within the asci are here thread-like (Fig. 207, G), so that they are readily distributed by the wind. If caught by the stigma of a Grass-flower the spores germinate and the hypha grows down through the style into the ovary, thus bringing about a fresh infection.

By slow degrees the contents of the ovary are replaced by a dense hyphal mass with deep surface furrows (Fig. 207, B, upper part). From the ends of the superficial hyphæ large numbers of minute oval conidia are budded off (Fig. 207, C), and at the same time the surface secretes a sugary liquid. This attracts insects, to whose bodies the conidia adhere, and so a rapid spread of the disease from flower to flower is brought about. Later in the summer the production of conidia ceases and the outer hyphæ blacken, whereby the resting sclerotium is formed.

The bright red pustules of *Nectria* and the branched sclerotia of *Xylaria* (Fig. 205, A) harbour flask-shaped perithecia similar to those of the Ergot.

In some Ascomycetes reproduction by conidia is far more frequent than the formation of asci, as, for instance, in the two common Moulds *Penicillium* (Fig. 208, *a*, *b*) and *Eurotium* = *Aspergillus*, Fig. 208, *f*). Here the conidia are budded off in chains from the terminal branchlets of erect hyphæ which, in *Eurotium* (Fig. 208, *f*), are strongly swollen at their apices. Both Fungi also occasionally produce spherical ascus-fruits (Fig. 208, *d*), which arise from special sexual organs (Fig. 208, *c*), although it is doubtful whether any actual fusion of cell-contents occurs.

In the White Mildews (*Erysiphaceæ*)[2] formation of conidia

[1] Similar sclerotia occur, as resting-stages, in the life-cycle of several other Ascomycetes, e.g. *Sclerotinia* (Fig. 205, E), a close ally of *Peziza*, whose cup-shaped apothecia arise from the sclerotia.

[2] The Mildews are the cause of many familiar diseases of cultivated plants, as instances of which may be mentioned the Gooseberry Mildew (*Sphaerotheca mors-uvæ*), the Rose Mildew (*S. pannosa*), *Erysiphe polygoni* (on Field Peas and

is again relatively common. The mycelium in these parasites develops externally, on the surface of the leaf (Fig. 209, *b*), the haustoria alone penetrating into the epidermal cells. The mildewed appearance is usually due to the extensive production of chains of conidia from the ends of unbranched upright hyphæ (Fig. 209, *c*), such chains being very striking in the Mildew

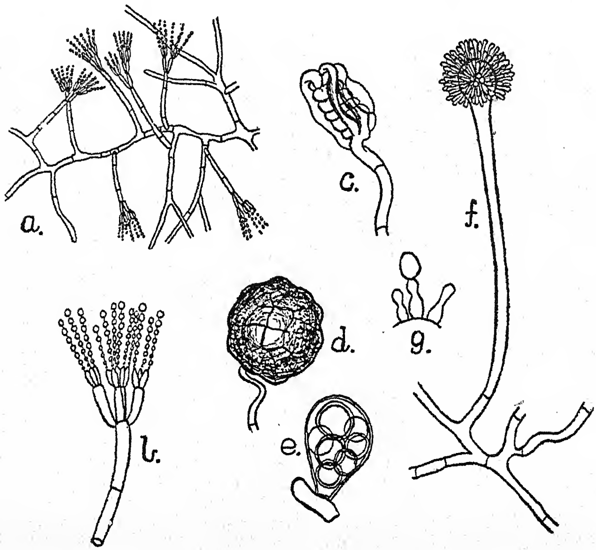


FIG. 208. *a–b*, *Penicillium*. *a*, Small part of mycelium with conidiophores; *b*, One of the latter enlarged. *c–g*, *Eurotium* (*Aspergillus*). *c*, Very early stage of fruit-formation, showing the coiled hypha (female organ) from which the asci arise; *d*, Mature fruit; *e*, An ascus from the interior of the same; *f*, Conidiophore; *g*, Small part of apex of same, showing the way in which the conidia are budded off. (*a* and *b*, after Brefeld; the remainder after De Bary.)

commonly found on Forget-me-not leaves (due to a species of *Oidium*). Later in the season many of these Fungi develop numerous small dark specks (Fig. 209, *a*), the ascus-fruits, on the greyish-white mycelium. Under the microscope they are seen to be almost spherical structures, provided with very diverse hair-like appendages and without an aperture (Fig. 209, *b*). The hard black wall ruptures irregularly, exposing one or more small asci (Fig. 209, *e*).

Cucumber), and *E. graminis* (on Wheat). Many so-called Mildews do not, however, belong to the Ascomycetes, but are Phycomycetes, whose richly branched conidial-bearing hyphæ give a whitish appearance to the leaves; such are the Cabbage Mildew (*Peronospora parasitica*) and Grape Mildew (*Plasmopora viticola*).

In the Hop Mildew (*Sphaerotheca castagnei*) it has been established that the fruit arises from club-shaped *sexual organs* of

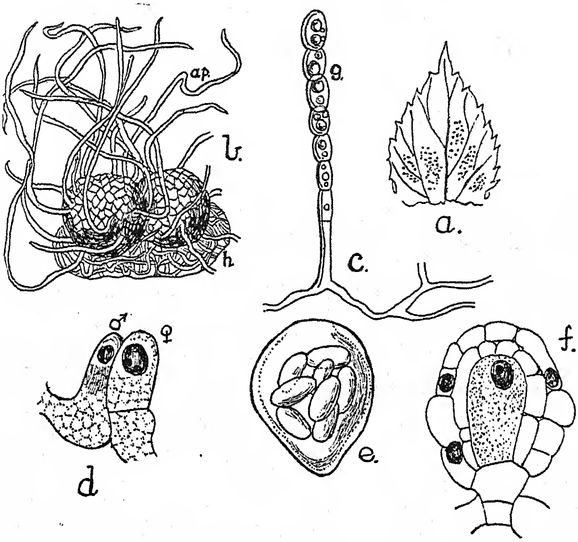


FIG. 209. The Hop Mildew (*Sphaerotheca castagnei*). *a*, Part of the leaf of the Hop, with the ascus-fruits; *b*, Small part of the surface, greatly magnified, showing the superficial hyphæ (*h.*) and two ascus-fruits, each with numerous long appendages (*ap.*); *c*, Production of a chain of conidia (*g.*); *d*, Sex organs in apposition; *e*, Ascus; *f*, Young fruit. (*a*, after Wettstein; *b*, *c* and *e*, after Tulasne; *d* and *f*, after Harper.)

unequal size, the larger functioning as the female (Fig. 209, *d*). Their tips become closely adpressed, but, owing to the great difficulty of establishing such facts, there exists a marked difference of opinion as to whether or not there is a nuclear fusion like that described for the Phycomycetes. The same doubt attaches to many instances of sexual fusion that have been investigated in the Ascomycetes. Since, however, a production of sexual organs has been observed in some species, prior to the formation of each kind of ascus-fruit encountered in this group, the view is generally held that all its members are to

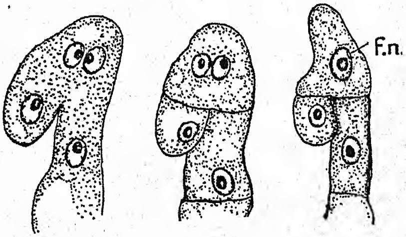


FIG. 210. Ascus-formation in *Pyronema confluens*, slightly diagrammatic (based on Harper). *F.n.*, fusion-nucleus in cell from which ascus will arise.

be regarded as being descended from Fungi which exhibited a sexual process, now often functionless. In fact, in most Ascomycetes no traces of sexual organs are to be found.

As a result of nuclear division in the cells of certain hyphæ which, when sex organs are present, arise as outgrowths from the female organ, binucleate cells are produced. The binucleate cell is commonly the penultimate cell of a crozier-shaped hypha and the first step in the development of an ascus consists in the fusion of the two nuclei. This is regarded by some as giving the same stimulus as a sexual fusion. The single nucleus thus produced undergoes successive division into eight, whereupon membranes are formed independently around each nucleus and the adjacent cytoplasm, so that eight ascospores are cut out; a small portion of the cytoplasm remains, however, which is not incorporated in the latter. These stages in the formation of the asci are to be found in the subhymenium.

The *Basidiomycetes* are altogether devoid of sexual organs. They are likewise characterised by a special mode of spore-formation in which a definite number of spores (usually 4) is constricted off from the mother-cell. This large group includes many saprophytes, familiar examples being the Mushroom (*Psalliota*, Fig. 213), various Toadstools (e.g. *Coprinus*, *Boletus*), Puff-balls (*Lycoperdon*, Fig. 216, B), etc. The mycorrhizal Fungi of higher plants mostly belong to this group. The Smuts (Ustilagineæ) and Rusts (Uredineæ) are peculiar members of Basidiomycetes.

The *Rusts* are of special importance as being the cause of many serious diseases of crops, and of these the Rust of Wheat (*Puccinia graminis*) is, unfortunately, all too common. Like many other Uredineæ, it possesses a very complicated life-history, whose phases occur on two different hosts. In summer the parasite attacks the leaves and stems of various Grasses, and betrays its presence by the development of orange-coloured streaks upon them. These are due to clusters of unicellular thick-walled spores (summer- or *uredo-spores*) of an orange colour, beset with numerous minute spines; each spore arises at the end of a projecting hypha (Fig. 211, B, *u*). After detachment they may be blown by the wind on to another appropriate Grass, whereupon hyphæ grow out through special thin areas of the wall (Fig. 211, F), to start a fresh generation of the Rust. In this way the disease rapidly spreads during the summer months.

Towards autumn special winter- or *teleuto-spores* are produced, and these remain dormant in the soil until the following spring. The formation of teleutospores is evidenced by a darkening of the

streaks on the Grass-leaves. These are now caused by clusters of bicellular spores (Fig. 211, D), again borne singly at the ends of projecting hyphæ, and provided with a thick dark brown membrane (Fig. 211, B, *t*) which has a thin germinal pore in each cell.

With the advent of spring both cells of the teleutospore put out

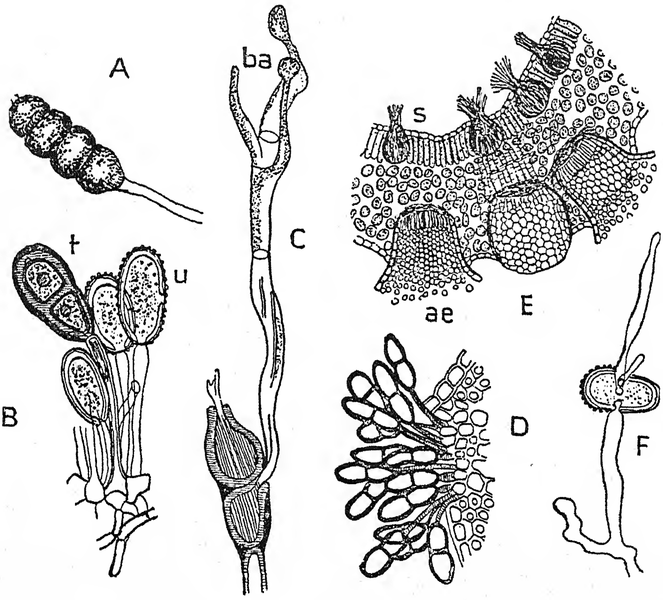


FIG. 211. A, Teleutospore of *Phragmidium*. B–F, Rust of Wheat (*Puccinia graminis*). B, Group of uredospores (*u.*) and one teleutospore (*t.*). C, Germinating teleutospore (only the hypha growing from one of the two cells is shown at its full length), with developing basidiospores (*ba.*). D, Group of teleutospores, seen in section of leaf of Wheat. E, Section of Barberry-leaf, showing æcidia (*ae.*) in two stages of development, and spermogonia (*s.*). F, Germinating uredospore. (B, D and F, after De Bary; C, after Tulasne; E, after Sachs.)

a short hypha composed of four cells (Fig. 211, C), each of which gives rise to a process bearing a small spherical spore (*basidiospore, ba.*). The latter is only capable of further development if carried by the wind to a plant of the Wild Barberry (*Berberis vulgaris*). In that event a mycelium is produced within the new host, and the presence of the disease is soon manifested by the appearance, usually on the under-surface of the leaf, of groups of small orange-coloured cups (the cluster-cups or *æcidia*, Fig. 212). The minute specks, recognisable on the upper surface of the leaf, are caused by small flask-shaped cavities (*spermogonia*, Fig. 211, E, *s.*)

containing hyphæ from the ends of which small reproductive cells are budded off.

In a vertical section (Fig. 211, E) the hyphæ of the æcidium (*ae.*) form a compact bounding wall, whilst from the dense interwoven mass at the base arises a palisade-like hymenial layer whose hyphæ bud off rows of orange-coloured *æcidiospores*, separated by flat sterile cells. The spores, if carried by the wind to Wheat or other Grasses, give rise to a new uredo-form.

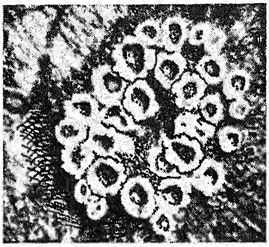


FIG. 212. Group of cluster-cups (æcidia) on leaf of *Ranunculus* (magnified about 5 times).

Whilst the cells of the mycelium in the Barberry-leaf producing spermogonia are uninucleate, that forming the young æcidium is binucleate, and the resulting spores are similarly provided with two nuclei. The reproductive cells formed within the spermogonia can apparently fuse with certain branched hyphæ in spermogonia derived from another mycelium. A binucleate mycelium thus results which gives rise to the æcidia. Assuming these observations to be correct, the Rust Fungi would also appear to exhibit heterothallism. The binucleate condition persists throughout all the uredo-forms, and the cells of the young teleutospores show the same feature, but fusion of the nuclei occurs as the latter mature.

The existence of the Fungus on different host-plants, at different stages of its life-cycle, is paralleled among animal parasites (*e.g.* Malarial Parasite, Tapeworm), and affords one means for the extermination of the disease, viz. by the eradication of one host. This is, however, only partially successful, since Wheat Rust occasionally appears in successive years, even where the Barberry does not grow (*e.g.* Australia), which is probably due to the survival of uredospores through the winter, or to the persistence of the Fungus in the tissues of winter-green Grasses. In some Rusts there is no uredospore phase (e.g. *Puccinia anemones* on the Wood Anemone), whilst in others (e.g. *Puccinia malvacearum* on the Hollyhock) only teleutospores are known. Another common Rust is *Phragmidium bulbosum*, causing purple spots on the leaves of the Blackberry. This has 3- or 4-celled teleutospores (Fig. 211, A).

Some of the Rusts exhibit very extreme specialisation in relation to definite host plants, possessing strains which, though morphologically identical, can only develop on one particular species (biologic strains). Others, however, can attack a variety of related hosts, and, in the continuance of a disease of cultivated crops, wild plants may often play an important part in bridging the interval of a rotation.

The Smuts (*Ustilagineæ*) are characterised by the sooty black mass of spores which are formed by the breaking up of the hyphæ into unicellular portions with a thick pigmented wall. They occur extensively as diseases of various Cereals (*e.g.* Oats, Wheat, Maize), infesting either the leaves (Fig. 216, G) or the ovaries.

The common Mushroom (*Psalliota campestris*) affords an

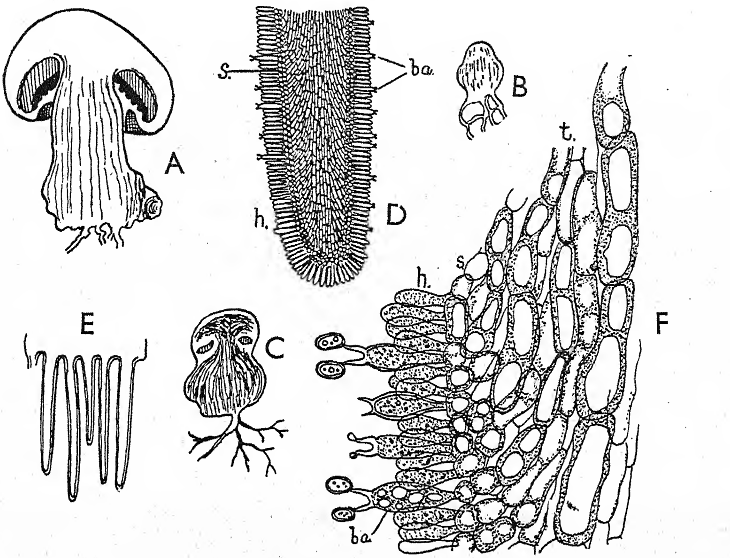


FIG. 213. The common Mushroom (*Psalliota campestris*). B, C and A, Successive stages in the development of the fructification (in A the annulus is distinct, but yet unruptured). E, Transverse section through small part of cap, showing gills. D, One of the latter enlarged. F, Surface of a gill, in section, highly magnified. *ba.*, basidium; *h.*, hymenium; *s.*, subhymenium; *t.*, large cells of middle of gill. (After Sachs.)

example of the more typical Basidiomycetes. The mycelium, which inhabits soil rich in humus, and is present in considerable amount in so-called Mushroom spawn, is composed of binucleate cells. The hyphæ, as in many other Basidiomycetes, tend to be interwoven in bundles, so that the mycelium appears thicker and coarser than in other Fungi. The overground edible portion is the reproductive body which first appears on the mycelium as a knob-like swelling (Fig. 213, B) composed of densely interwoven hyphæ, but later, as it gradually enlarges, broadens out at the top (Fig. 213, C, A). In the mature condition it consists of a stalk and an umbrella-shaped cap (cf. also Fig. 215, A, *cp.*), with a large number of radiating plates or gills (*g*) on the under surface, which

bear the *hymenium*. A little way below the cap the stalk is surrounded by a membranous ring of broken tissue (the *annulus*, *a*) which, before the expansion of the cap, extended continuously from the edge of the latter to the stalk, thus constituting a protection for the developing gills (Fig. 213, A).

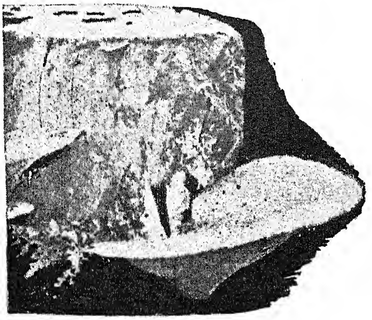


FIG. 214. The Bracket Fungus (*Polyporus squamosus*). [Photo. E. J. S.]

In a vertical section through the cap (Fig. 213, A, E) the middle of each gill (D, F) is seen to consist of longitudinally arranged hyphæ. These are composed of rather large cells (*t.*), and diverge at their ends to form a round-celled sub-hymenium (*s.*) and the superficial palisade-like hymenium (*h.*). The latter comprises two kinds of club-shaped hyphal terminations: some, the *basidia* (*ba.*), bear at their apex two, or four, short processes, from the end of each of which a *basidiospore* is formed, whilst the others are purely sterile. This method of spore-formation is that characteristic of Basidio-mycetes generally, four being the usual number produced. The colour of the spores varies considerably in different species.

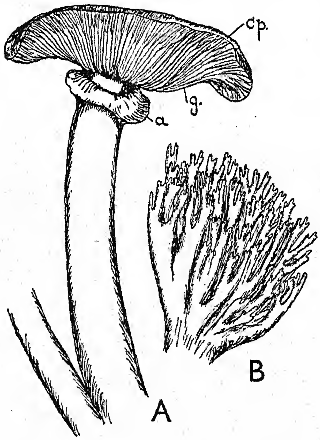


FIG. 215. A, Toadstool (*Agaricus*), slightly reduced. B, *Clavaria*. *a.*, annulus; *cp.*, cap; *g.*, gills.

The enormous production of spores in this and other similar Fungi can be gauged by placing the mature caps, with the gills downwards, on a sheet of white paper, when, after a short time, the outline of each gill will be marked by the spores which have been shed. It has been estimated that a moderate-sized specimen will produce some 1,800,000,000 spores, and other allied species form spores in even greater profusion.

In the genus *Boletus*, whose fruit-body has the same general form as that of the Mushroom, the under side of the cap presents the structure of a honeycomb, consisting of a multitude of vertical tubes, the inner surfaces of which are lined with hymenium (Fig. 216, E).

A similar construction is seen in the Bracket Fungus (*Polyporus squamosus*, Fig. 214), whose thick tough fruit-bodies are commonly found on decaying tree-trunks, to which they are attached along one side of the cap (Fig. 221). Some of the related Fungi (e.g. *Dædalea quercina*) have woody fructifications which may persist for several years, whilst others are dangerous parasites to forest trees (e.g. *Armillaria mellea*, Fig. 220). In *Hydnum* (Fig. 216, F) the

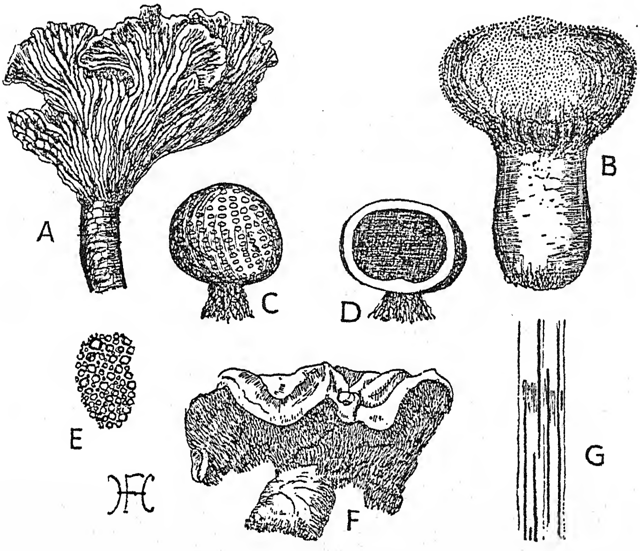


FIG. 216. Various Basidiomycetes. A, *Cantharellus*. B, *Lycoperdon*. C, D, *Scleroderma vulgare* (C, entire; D, in vertical section, showing the wall and the dark mass of contained spores). E, Surface-view of small part of hymenium of *Boletus*. F, *Hydnum repandum*. G, *Ustilago longissima* (on leaf of *Glyceria aquatica*).

hymenium covers the numerous pointed projections arising from the under side of the cap.

Further instances of the diversity of fruit-bodies in the Basidiomycetes are furnished by the purple encrusting fruits of the Fungus responsible for the Silver-leaf disease of the Plum (*Stereum purpureum*), the Puff-balls (*Lycoperdon*, Fig. 216, B), whose spores form a powdery mass within the pear-shaped fructification, and the Coral Fungus (*Clavaria*, Fig. 215, B), where the fruit-body is richly branched and bears the hymenium over its entire surface (cf. also Fig. 216).

The young basidium is binucleate, but these nuclei fuse prior to the production of basidiospores. The binucleate condition

usually arises, long before the formation of fruit-bodies, through the fusion of two hyphæ belonging to mycelia of different strains (heterothallic), and it is only as a consequence of this that fertile fruit-bodies are usually produced.

In conclusion, a brief reference must be made to the Slime Fungi (*Myxomycetes*), whose relation to other Thallophyta is exceedingly obscure; in some respects they show resemblances to Protozoa, although the methods of multiplication recall those habitual among lower plants. The Slime Fungi are most evident in damp weather, when the large naked protoplasmic masses (*plasmodia*), constituting the vegetative phase, creep out from the crevices of the decaying tree stumps, humus, or other substratum. Small, often rounded sporangia, containing numerous spores, are formed, especially in the autumn, and are sometimes very conspicuous owing to their brilliant colouration (*e.g.* the yellow-coloured Flowers of Tan, common on tanner's bark). The group also includes some parasites, one of the most noteworthy (*Plasmodiophora brassicæ*) being that responsible for the disease known as "Finger and Toe" in Cabbages, etc. (Fig. 217).

[For more detailed treatment of the Fungi, see H. C. I. Gwynne-Vaughan and B. F. Barnes, *The Structure and Development of the Fungi*, 2nd edit., Cambridge University Press, 1937 (449 pp.); H. M. Fitzpatrick, *The Lower Fungi (Phycomycetes)*, McGraw Hill Book Co., 1930 (331 pp.); E. A. Gaumann, *Comparative Morphology of Fungi* (transl. by C. W. Dodge), McGraw Hill Book Co., 1928 (701 pp.); E. J. Butler, *Fungi and Disease in Plants*, Thacker, Spink & Co., 1918 (547 pp.), a particularly valuable general account in the introductory chapters. For taxonomic works, see p. 579.]

CHAPTER XXIX

PHYSIOLOGY OF FUNGI, LICHENS, BACTERIA

MANY of the Fungi play a very important rôle in the economy of nature. The *saprophytes*, in association with Bacteria, are largely responsible for the decomposition of vegetable remains, and without them the whole surface of the earth would become buried under the bodies of plants and animals. Through their agency the material locked up in the raw humus of the soil is transformed into simpler chemical compounds, and rendered available for the use of higher plants. A striking instance of this function is afforded by those Fungi, responsible for the decomposition of humus, which are intimately associated as a *mycorrhiza* with the underground organs of Flowering Plants (cf. p. 218 and Fig. 63). The processes of decay initiated by saprophytes are, however, often detrimental to the interests of man, as in the Basidiomycete *Merulius lacrymans* responsible for so-called "dry rot" of timber, and the diverse and almost ubiquitous Moulds which all too readily develop upon articles of food.

The *parasitic species* [1] frequently do great damage to cultivated plants and to animals. In some the parasite sooner or later brings about the death of its host (*e.g.* Silver-leaf Disease of Plum), but more commonly (*e.g.* Mildew, Rust) the diseased plant, though injured, continues to live as an unhealthy individual supporting the parasite which grows at its expense. A considerable number of parasites (facultative parasites) can also exist as saprophytes, so that they remain alive after the host has died (e.g. *Pythium* and many Smuts). Conversely, certain saprophytes (e.g. *Mucor*) can occasionally act as parasites, generally after access has been obtained at a point of injury. The so-called wound-parasites (*e.g. Nectria*, a species of which causes Coral-spot Disease of various trees) belong to this category, though their saprophytic phase is of short duration. The majority of Fungi, however, are either strictly saprophytic or strictly parasitic (obligate parasites).

[1] For a more detailed treatment, see F. T. Brooks, *Plant Diseases*, Cambridge Univ. Press, 1928 (386 pp.); J. Eriksson, *Fungous Diseases of Plants* (transl. by W. Goodwin), Baillière, Tindall & Cox, 2nd edit., 1930 (526 pp.); and the work of Butler, cited on p. 334.

Often special conditions, such as excess of moisture (e.g. *Pythium*), the general state of health of the host, or accidental injuries to the latter, may be instrumental in bringing about the attacks of parasitic Fungi. Epidemics of such widespread diseases as the Potato Blight and the Gooseberry Mildew have, for instance, been associated with particularly damp warm seasons. Fungi are rarely pathological in man, but it may be mentioned that various skin diseases (*e.g.* Ringworm, *Favus*) are due to Fungi.

Owing to the small size of the spores, Fungi often become widely disseminated by the wind, but so far as can be gauged by the careful study of the spread of plant diseases due to Fungi, *infection* by wind-borne spores seldom occurs beyond a few miles. Long-distance carriage is generally to be attributed to transport in infected plants or plant-fragments, through human or other agency, hence the value of careful inspection and control of imported horticultural produce.

In dealing with the Rust Fungi, mention was made of the fact that a particular species or strain of these parasites may be so specialised as to be able to attack only one particular kind of host, and the same is true of the Mildews. There is thus often a difference, with regard to *susceptibility* to a certain disease, between the various races of a cultivated plant; for instance, some varieties of Potato and Wheat are immune to Blight and Rust respectively, and would tend to be grown in regions in which these Fungi were known to be prevalent. Much has also been done by the production of immune hybrids (cf. p. 589) between immune and non-immune races. The ravages of a disease may decrease in intensity after it has been rampant for some years, the host presumably becoming adapted to the presence of the parasite; thus the Hollyhock Rust (*Puccinia malvacearum*), when first introduced into Europe about 1870, played great havoc with its host, but now, though Hollyhocks are still commonly attacked, they do not appear to suffer appreciably.

There are other plant diseases which are caused by the presence of what are known as *viruses*. Among the more familiar of these are the mosaic diseases of Tobacco, Raspberry, and Potato, which produce a mottled appearance of the foliage. The nature of a virus is not certainly known, but the causal agent whether living or non-living is extremely small. Potato virus particles may be 100 millimicrons [1] in diameter, whilst a virus of the Tomato consists of units less than 25 millimicrons, so that they will pass through the finest filters. Other filter-passes are responsible for diseases in animals. If the virus is non-living, then its presence must stimulate the attacked cells to produce more of the virus, as in

[1] A millimicron is a millionth of a millimetre.

an autocatalytic reaction. Recent evidence indicates that some viruses at least are probably crystalline in nature.

The disease is transmitted by sap-sucking insects (insect-vectors), such as Aphides and plant Bugs. An interesting feature of virus disease is the discovery that there are various types of virus causing the same disease and that the presence of two of these causal agents in a host at the same time may have no apparent effect, although either by itself would be accompanied by symptoms of disease.[1]

FIG. 217. *Sisymbrium officinale* and Brussels Sprouts attacked by "Finger and Toe" (*Plasmodiophora brassicæ*). [Photo. E. J. S.]

Artificial *control of fungal diseases* is accomplished by diverse means, but for successful treatment a knowledge of the life-history of the parasite is essential. The method of treatment varies according as the parasite attacks the overground or underground organs of the host. Several of the Fungi considered in the last chapter (*e.g.* Potato Blight) afford instances of the former mode of attack. Diseases of the subterranean parts are exemplified by the pernicious Wart Disease of the Potato, due to a lowly Fungus of a peculiar kind, and that known as Finger and Toe (Fig. 217 and p. 334), which attacks Turnips, Cabbages, etc., causing irregular swellings upon the root-system.

One of the remedies most commonly employed against Fungi infesting the overground parts is spraying with a *fungicide* which, while deleterious to the parasite, leaves the host practically unharmed. For this purpose Bordeaux mixture, consisting of a solution of copper sulphate and slaked lime, is one of the most popular. Where the disease is subterranean, application of unslaked lime is often successful, as, for instance, in the treatment of Finger and Toe. Such diseases are, however, far more difficult

[1] For further details, see K. M. Smith, *Plant Viruses*. Methuen, 1935 (107 pp.).

to eradicate than those which develop overground. They are often best counteracted by growing only such crops, in the infected soil, for several seasons in succession, as are not attacked by the parasite in question. For many diseases no adequate remedy has yet been discovered, and the only advisable procedure in the event of an outbreak of disease, is to burn all infected plants, so as to prevent the spread of the parasite.

Fungi are, however, not only of importance in causing decay and disease, but also afford several greatly prized articles of diet (*e.g.* Mushrooms, Truffles, Morels, etc.), although their actual food-value is probably small. The great majority of the British Basidiomycetes are innocuous, but there are a certain number of species, some very widely distributed, which harbour deadly *poisons* (alkaloids, etc.), and such Fungi are by no means always highly coloured. Examples are the Fly Toadstool (*Amanita muscaria*) and the Death Cap (*Amanita phalloides*). An edible Fungus is seen in the so-called Vegetable Caterpillar (*Cordyceps*), where a sclerotium completely replaces the internal organs of the larva; this parasite is extensively cultivated in parts of the East and used as a condiment. Fungi are not often employed in medicine, except for the powdered sclerotium of the Ergot (*Claviceps*) which contains a nitrogen base having the property of causing muscular contraction.

The production of most alcoholic beverages is due to the activity of Yeasts (*Saccharomyces*), peculiar members of the Ascomycetes. The Yeast-plant (Fig. 222) consists of oval cells, which are either isolated (*a*) or adhere together (*c*). The thin-walled cells contain a large central vacuole (Fig. 222, *e*, *va*), and, in contact with the latter at one point, a nucleolus with surrounding chromatin (*n*), which become apparent on staining the living cells with a dilute aqueous solution of methylene blue; vacuole, nucleolus, etc., together probably represent the nucleus. The Yeast-cells often contain large glycogen-vacuoles (*g.*), as well as small bodies (*v*), stained deeply by methylene blue, and known as volutin-granules, which appear to constitute another kind of reserve.

When a cell has reached a certain size, it gives rise to a small outgrowth (Fig. 222, *b*) which slowly enlarges and assumes the form of the parent, from which it becomes separated by gradual constriction; if this process of *budding* takes place rapidly, the cells do not immediately separate, and thus groups (Fig. 222, *c*) are formed. A resting-stage also occurs, as when Yeast is grown on the surface of a raw Potato; under these circumstances the cell-contents undergo division, usually into two or four parts, each

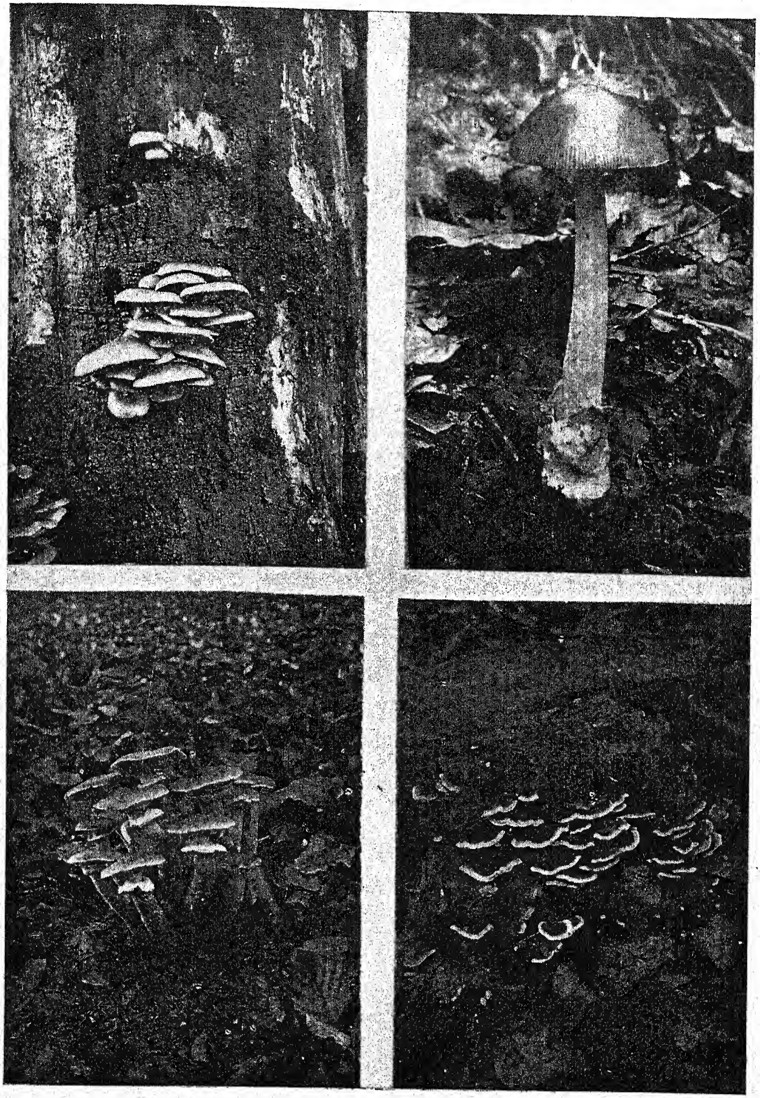


FIG. 218. *Pleurotus ostreatus.* FIG. 219. *Amanitopsis vaginata.*
FIG. 220. *Armillaria mellea.* FIG. 221. *Polystictis versicolor.*
[All after photos by Mr. E. M. Cutting, M.A.]

surrounded by a thick wall (Fig. 222, *d*). This formation of ascospores may be preceded by conjugation of Yeast-cells.

There are a number of different species of Yeast which ferment various sugars and split them up into alcohols (mainly ethyl alcohol) and carbon dioxide. The chemical change is brought about by an enzyme-group known as *zymase* (cf. p. 83) which can, with some difficulty, be extracted from the cells; in addition, the latter contain invertase and other enzymes. The mode of action of zymase is complicated and not yet fully understood, but

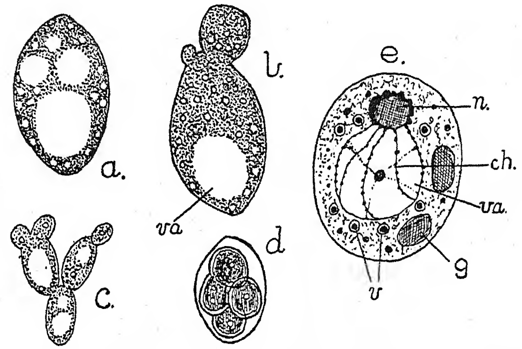


FIG. 222. Yeast (*Saccharomyces*). *a–c*, Various individuals, showing general form and multiplication by budding; *d*, Individual containing ascospores; *e.*, Cell-structure. *ch.*, chromatin threads; *g.*, glycogen vacuole; *n.*, nucleolus with surrounding chromatin; *v.*, volutin granules; *va.*, nuclear vacuole. (*a–d*, after Wettstein; *e*, after Wager.)

it is known that *fermentation* depends on the contemporary presence of phosphates (cf. p. 86). The alcohol present in beer, wine, etc., is formed by the action of Yeasts, while the carbon dioxide simultaneously evolved is compressed into cylinders and sold as a by-product. In the manufacture of beer, malt (*i.e.* germinated Barley) is treated with hot water and supplies part of the sugar, various other sugars being used according to local practice. Hops are added to the liquid to provide the peculiar flavour, and the whole of this "wort" is then fermented in vats.[1] The success of brewing largely depends upon the employment of pure races of Yeast and the realisation of the right temperatures at the different stages of the process; a small supply of oxygen has also been shown to be favourable to active fermentation.

[1] If all the starch in the malt is allowed to undergo conversion into sugar, and the fermented product is distilled, whisky results; brandy is similarly obtained by distilling the alcohol from fermented grape-juice. The Japanese *saké* is obtained by the fermentation of rice.

The energy liberated in the fermentation of sugars enables Yeast to thrive and grow when, apart from the sugars, only inorganic food-materials are supplied. Here, therefore, chemical energy is utilised in synthesis. The process of alcoholic fermentation shows much resemblance to anaerobic respiration (cf. p. 239), but here the compounds broken down are outside and not within the organism, so that no loss of weight is involved. It may be added that Yeasts are not alone among Fungi in fermenting sugars, since spores of *Mucor*, for example, if placed in a sugary liquid, will reproduce by budding and cause alcoholic fermentation, forming so-called *Mucor*-yeast. Another manifestation of energy liberated by fungal activity is the luminescence of the hyphæ of species such as *Armillaria mellea* (Fig. 220).

We have already noted that a parasitic Fungus may sometimes do very little harm to the host, and such instances are but a step removed from those in which the balance, between the Fungus and the organism with which it is associated, is so perfect that both are mutually benefited. Such a condition is found in the *Lichens*,[1] whose body is composed of algal cells embedded in a weft of fungal hyphæ. Lichens, with but few exceptions, are subaerial, being commonly found on peaty soils, rocks, tree-trunks, old walls, etc. In conjunction with various Algæ and Mosses, Lichens play an exceedingly important part in the primary colonisation of rock surfaces and of other ground laid bare of vegetation, being conspicuous, for instance, among the early vegetation of burnt heaths. The black-coloured blotches, which are such a familiar sight on the pebbles of a shingle-beach, are due to various Lichens (e.g. *Rhizocarpon confervoides*, Fig. 223, C), which are here the first colonisers.

The shape of the thallus is very diverse, and, as a general rule, almost entirely determined by the Fungus. It most commonly takes the form of flat, lobed expansions which are often almost circular (e.g. *Parmelia*, *Xanthoria*, Fig. 223, D). Other frequent types are those exhibiting repeated branching (Fig. 223, B); in such the segments may be upright (*e.g.* Iceland Moss, *Cetraria islandica*, Fig. 225) or hanging (e.g. *Usnea*, Fig. 223, A). The thallus is sometimes highly gelatinous, so that it is much more conspicuous in wet than in dry weather (e.g. *Collema*).

The Algæ found within the thalli of Lichens are similar to forms

[1] For a more detailed account of Lichens, see A. Lorraine Smith, *Lichene*, Cambridge Bot. Handbooks, 1921 (464 pp.); and F. Tobler, *Die Flechten*, G. Fischer, Jena, 1934 (84 pp.), the latter the most recent account of their biology and reproduction. For taxonomic works, see p. 579.

which grow independently in terrestrial habitats; examples are afforded by the unicellular green *Trebouxia* (p. 281, in the Lichen *Cladonia*) and the filamentous blue-green *Nostoc* (found in *Peltigera*). The Fungi concerned are, on the other hand, unable to lead an independent existence in nature, and are only normally capable

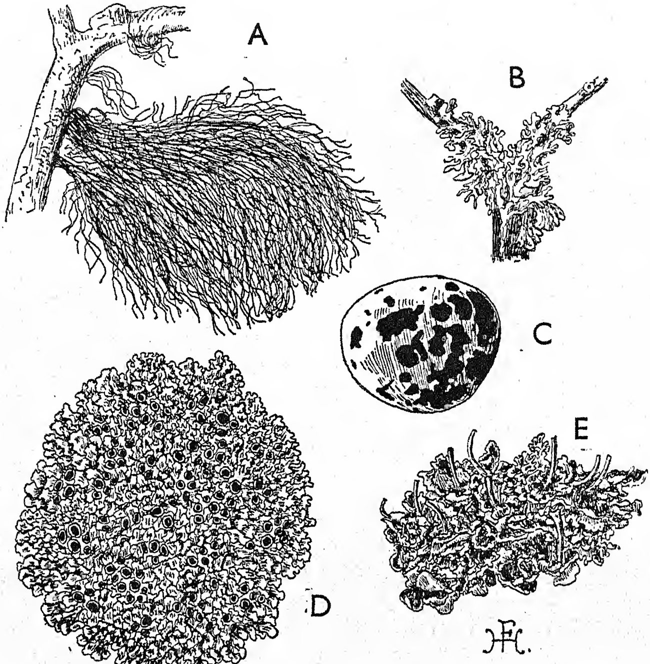


FIG. 223. Various common Lichens. A, *Usnea barbata*. B, *Parmelia physodes*, on twig. C, *Rhizocarpon confervoides*, on pebble. D, *Xanthoria parietina* (showing numerous apothecia). E, *Cladonia* sp., showing the upgrowths on which the apothecia are borne.

of growth when associated with one particular Alga. Different physiological races of the same species of Alga may, however, be coupled with several different Fungi to form as many distinct Lichens, but each Fungus has only one algal associate. It has even proved possible to produce a Lichen artificially by sowing the spores of its fungal constituent among the appropriate algal cells. The vast majority of Lichen Fungi belong to the Ascomycetes, as shown by their fructifications, which closely resemble small rather flattened *Peziza*-cups (Fig. 223, D). In *Cladonia* (Fig. 223, E), where the thallus itself is often inconspicuous, the

reddish apothecia are borne on the edges of variously shaped upgrowths.

Since the hyphæ at the two surfaces of the thallus are usually densely compacted and thick-walled (Fig. 224, C), the Alga (*al.*) embedded in the interior is well protected during times of drought. As a general rule, moreover, tufts or isolated hyphæ project from

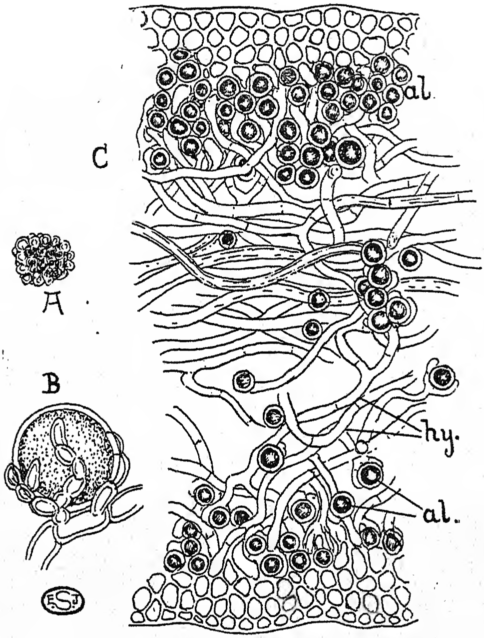


FIG. 224. A, Soredium, and C, Section through the thallus, of the Lichen *Xanthoria parietina*. *al.*, algal cells; *hy.*, fungal hyphæ. B, An algal cell from the Lichen *Cladonia*, illustrating the intimate relation between it and the fungal hyphæ. (B, after Bornet.)

the underside into the substratum, absorbing moisture which is held there by capillarity, and thus the algal cells are kept supplied during dry periods. In Lichens growing on rocks, the penetration of these hyphæ is facilitated by the secretion of solvents, and it is to this property that such Lichens owe their important rôle in the disintegration and colonisation of bare rock-surfaces.

Whilst the Alga thus obtains protection and a supply of moisture, the Fungus no doubt profits by absorbing part of the photosynthetic products of the former, with whose cells some of its hyphæ come into intimate contact (Fig. 224, B). The hyphæ are, in fact, stated sometimes actually to penetrate the algal cells, so

that the partnership borders closely on parasitism. Apart from this intimate relation, most of the enveloping hyphæ are loosely arranged, so that a well-marked system of intercellular spaces admits of the inward diffusion of carbon dioxide (Fig. 224, C, *hy.*). In transverse sections the algal cells are seen as patches scattered throughout the thallus (e.g. *Collema*) or occupying definite zones (e.g. *Xanthoria parietina*, Fig. 224, C).

The association between Alga and Fungus is paralleled by the so-called "green cells" found in several aquatic animals (*e.g.* fresh-water Sponges, *Hydra viridis*); these are due to unicellular Algæ (species of *Chlorella*, etc.), and in all such partnerships between plant and animal there appears to be a mutual benefit (symbiosis). In this connection it may be noted that Algæ are found commonly inhabiting the intercellular spaces of certain higher plants (*e.g.* Duckweed, the Liverwort *Anthoceros*), but here the Algæ appear to be nothing more than "space-parasites" obtaining protection.

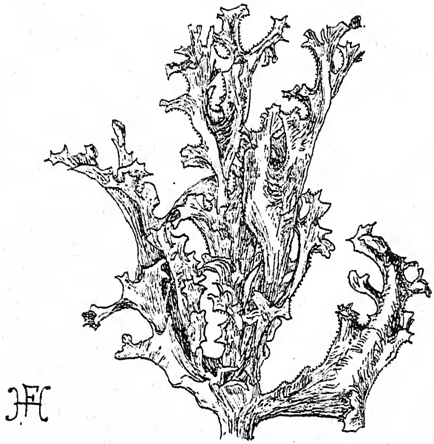


FIG. 225. Iceland Moss (*Cetraria islandica*), part of a large specimen, about natural size.

The ordinary cup-like fructifications of Lichens originate from the Fungus, and the resulting ascospores reproduce the latter only, so that germination of the spores must take place in the neighbourhood of the appropriate Alga, if a fresh Lichen is to be formed. But multiplication involving the dual organism is the rule; small parts of the thallus, or algal cells surrounded by interlacing hyphæ, become detached, and when this takes place on a large scale the surface of the thallus acquires a powdery appearance. The individual granules (so-called *soredia*, Fig. 224, A), being distributed by the wind, afford a rapid means of propagation of the dual organism.

The bright colours of many Lichens are due to the presence of pigments which are remarkable for their "fast" character, and have been employed in dyeing. The well-known chemical indicator litmus is obtained from species of *Roccella*. Iceland Moss (*Cetraria islandica*, Fig. 225), which forms a slimy fluid when boiled with water, is used as an invalid food.

The *Bacteria*[1] constitute an extremely important group of Thallophyta whose relationships are very obscure. The majority of species are colourless unicellular plants of extremely small size. The larger specimens are not more than 1/100th mm. in length and about one-tenth as wide, whilst the globular forms average 1/1000th mm. in diameter. Some are so small as to be almost, if not quite, invisible under the highest powers of the microscope. They occur in almost every possible situation, and live under the most varied conditions. They are not killed by cold, and some can survive for many months at the temperature of liquid air. Whilst most die if heated to about 50° C., a few (*thermophilic Bacteria*) live in fermenting hay and manure heaps which, owing to their activity, may attain a temperature of 70° C.[2] Many Bacteria also inhabit the waters of hot springs.

Bacteria are rod-shaped (*Bacillus*, Fig. 226, *d*, *f*, *Bacterium*), spherical (*Micrococcus*), or curved (*Spirillum*, Fig. 226, *k*). The rod-shaped individuals may be joined end to end to form long filaments (Fig. 226, *d*), whilst the *Coccus*-forms may occur in chains (*Streptococcus*, Fig. 226, *b*), in cubical packets (*Sarcina*), or in irregular masses (*Staphylococcus*, Fig. 226, *a*). The individuals may be capable of movement owing to the possession of flagella, which are only visible after careful staining, or they may be devoid of these, and merely exhibit Brownian movement in correspondence with their minute dimensions. In the elongated forms the flagella are either situated in tufts at the two ends (*Spirillum*, Fig. 226, *k*), or else arise all over the body (*Bacillus*, Fig. 226, *e*, *f*), but there are some genera possessing only one or two flagella restricted to one end of the cell (*Pseudomonas*, Fig. 226, *l*).

Very little is known regarding the internal structure of the cells, and it is a matter of doubt whether or not they possess a true nucleus; plastids are of course absent. The cell-wall appears to consist of a protein, and may probably be regarded merely as a differentiated outer layer of the cytoplasm. The latter contains various substances, of which the commonest are glycogen (cf. p. 316), granules of volutin (p. 338), and fat-globules which appear as brighter specks in the cytoplasm.

Multiplication of the cells by *division*, under normal circumstances, ensues with great rapidity, often taking place once every hour, or even more frequently. In some of the elongated forms the daughter-individuals are separated off by a mere constriction

[1] See W. W. C. Topley and G. S. Wilson, *Principles of Bacteriology and Immunity*, Arnold, 1929 (1645 pp.). Various aspects of Bacteriology are dealt with in the comprehensive *System of Bacteriology*, published by the Medical Research Council in 1930 (several volumes).

[2] Hence the employment of manure for hot-beds, etc.

(e.g. *Bacterium* spp.), whilst in others the cell is subdivided by a transverse septum which subsequently splits down the middle. In certain Bacteria inhabiting water or other fluids, the daughter-individuals develop thick mucilaginous walls, and in consequence adhere together in vast numbers to form an, often iridescent, pellicle on the surface.

Bacteria survive unfavourable conditions by the formation of resting *spores*, produced within the cells by a localised concentration of the greater part of the protoplasm, which then stains

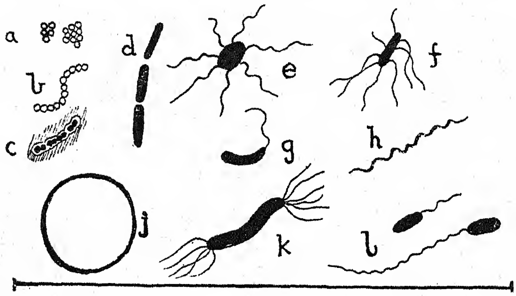


FIG. 226. Various Bacteria (magnified about 1000 times). *a*, *Staphylococcus aureus*; *b*, *Streptococcus pyogenes*; *c*, *Pneumococcus*; *d*, *Bacillus anthracis*; *e*, *B. typhosus*; *f*, *B. tetani*; *g*, *Microspora comma*; *h*, *Spirillum* of relapsing fever (possibly Protozoal); *k*, *Spirillum rubrum*; *l*, *Pseudomonas* spp. *j* represents a blood corpuscle on the same scale, and the line below, the width of a fine human hair, or about half the thickness of a sheet of newspaper. (*a–h*, from Muir and Ritchie; *k–l*, after Engler and Prantl.)

differently from the peripheral portion. This central region eventually becomes surrounded by a thick wall, and at maturity the remainder of the cell is often empty (Fig. 227, *b*, *c*). The spores are frequently located in special parts of the cell, giving the spore-forming individuals a characteristic appearance, as in *Bacillus tetani*, where they occupy a dilation of one end (Fig. 227, *a*). In certain forms (e.g. *Bacillus amylobacter*) more than one spore may be developed by each individual. Bacterial spores are often very resistant to extremes of temperature and can indeed sometimes (e.g. *Bacillus subtilis*) withstand prolonged boiling.

Most sorts of Bacteria live a free life in water, earth, etc. Many exert a very beneficial action in promoting decay and maintaining the circulation of nitrogen and carbon dioxide in nature, whilst a small number are extremely harmful, living as parasites on higher animals and plants, and causing such diseases as typhoid, cholera, plague, etc. Whilst some, such as *Bacillus subtilis*, which is found in infusions of hay, etc., require a free supply of oxygen (aerobic species), others, such as the organism

responsible for lock-jaw (*Bacillus tetani*), will grow in the almost complete absence of oxygen (anaerobic species).

It will be realised that the identification of the *pathogenic forms* (*i.e.* those causing disease), in particular, is of great importance. Owing, however, to the small dimensions of the individuals, it is as a rule impossible to identify the species by microscopic examination alone. Resource is therefore had to the various reactions of Bacteria under conditions of culture.

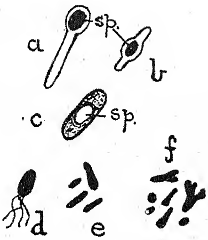


FIG. 227. *a–c*, Spore-formation in Bacteria. *a*, *Bacillus tetani*; *b*, *Bacillus* of malignant œdema; *c*, *Bacillus œdamitis*. *d–f*, Nitrogen-fixing Bacteria. *d*, *Azotobacter*; *e*, *Clostridium pasteurianum* sp.; *f*, *Bacillus radicicola*. (After Engler and Prantl, and Ellis.)

Bacteria can be grown in the laboratory on various artificial media, such as extract of meat, decoctions of fruit, etc. Under such conditions, and at temperatures suitable for each species, growth is very rapid, and a single organism soon multiplies to such an extent that the mass of its offspring is visible to the naked eye. In making cultures all the vessels and instruments employed are scrupulously cleaned and freed from live Bacteria (*sterilised*), either by heating to high temperatures (*e.g.* superheated steam in an autoclave) or by washing with special disinfectants, since even small quantities of dust are replete with bacterial spores.

The different kinds of Bacteria present in any material to be examined can be separated from one another and isolated by using the various culture media mentioned above, with the addition of gelatine or agar-agar (p. 293). A little of the material containing the organisms is well mixed with a considerable quantity of such a medium, liquefied by warming, so that the individual bacilli are widely separated from one another. On allowing the mixture to cool the Bacteria are immobilised; they soon grow, and each of the widely separated individuals gives rise to a small group (colony), visible to the naked eye, which can be transferred to another culture. In this way growths can be obtained which have arisen from single organisms (clones) and consist of one species only (*pure cultures*); in them the form of the Bacteria, their mode of growth, the formation of pigment (usually outside the cells) and other chemical substances, can be studied and the species identified.[1]

Some Bacteria are obligate parasites (*e.g.* the *Micrococcus* which causes spotted fever) and cannot live apart from their host, whilst others are facultative parasites (e.g. *Bacillus tetani*) and can live either

[1] Similar cultural methods are used for the study of Fungi and Algæ.

in earth, etc., or in the body of a Mammal. Each parasitic species can generally use only one or two species of Mammal as hosts; children, for example, do not have distemper, and dogs and cats do not have measles and chicken-pox. Similarly, *Bacillus carotovorus* causes "soft rot" of Carrot, but does not attack Parsnips.

The evil effects of parasitic Bacteria are due to poisons (*toxins*) which they produce; these are proteins in nature, and those which have been isolated are the most poisonous chemical substances known. The infected animal resists the invading organism, partly by the amœboid cells of the blood (leucocytes) which devour them, and partly by producing chemical substances which neutralise the toxins. The power of the body to make a successful resistance is much improved by practice. Hence one attack of an infectious disease often enables a person to destroy that particular bacillus at once if it gets into the body a second time, and so another attack of the disease is avoided.

A large number of Bacteria obtain energy [1] by bringing about processes of *fermentation*. Thus the Vinegar Bacteria (*Bacterium aceticum*, etc.) convert alcohol into acetic acid,[2] whilst the lactic acid Bacteria cause the souring of milk, changing the milk sugar (lactose) into lactic acid. Another product of bacterial activity is butyric acid, which is the chief cause of the rancid character of bad butter. The putrefaction of meat is likewise due to the agency of Bacteria, which decompose protein substances. Fermentation is often due to a group of organisms. Each type of cheese is the product of a definite bacterial and Fungus flora. The so-called ginger-beer plant, used in the manufacture of the beverage of that name, consists of a Yeast (p. 338) associated with certain Bacteria.

It is largely to Bacteria and certain Fungi that we owe the decomposition of the cellulose in dead leaves, etc., whereby undue accumulation is prevented, and the carbon is again brought into circulation as carbon dioxide. The processes of decay involved in the "retting" of fibres (*e.g.* Flax, Hemp, Jute), and the conversion of sewage are likewise brought about by Bacteria.

The nitrates of the soil, upon which plants are dependent for their supply of nitrogen, are continually being leached owing to their ready solubility, but the supply is always being reinforced by the action of Bacteria. The decay of plant and animal bodies, which is likewise due to bacterial agency, leads to the production

[1] In some cases part of this energy is dissipated as heat (cf. p. 345) or light (*e.g.* the phosphorescence of bad meat).

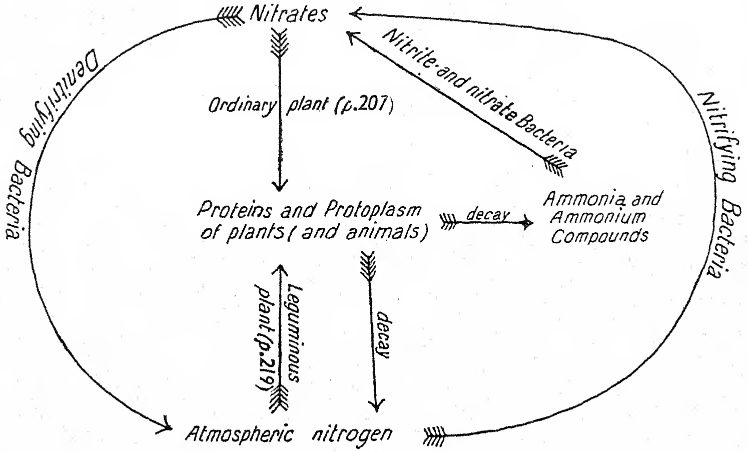
[2] In the commercial production of vinegar either wine or spirit is used as the raw material, and to these vinegar is added in order to introduce the necessary Bacteria.

of a large number of waste products, of which one of the most important is ammonia. The latter combines with the calcium carbonate to form ammonium carbonate, and this is oxidised to a nitrite by the so-called *Nitrite-Bacteria* which belong to the genus *Nitrosomonas*. The nitrites in their turn are converted into nitrates by the *Nitrate-Bacteria* (*Nitrobacter*), and in this way the ammonia, liberated by the decay of dead organisms, again becomes available to living plants.

By means of these oxidative processes the Bacteria in question gain the energy necessary for their vital activities. It has been found possible to cultivate them only in the absence of organic matter, but in nature the presence of the latter in the soil seems even to be beneficial. Nevertheless these organisms appear to be capable of building up organic substance from simple compounds, utilising for this purpose the energy obtained in the oxidative processes which they carry on. These nitrifying Bacteria cannot flourish in acid soils, or in such as contain an appreciable amount of free ammonia. This probably explains their paucity in many soils which are rich in acid humus (*e.g.* moorlands) or poor in lime. Where decay of organic matter takes place on a large scale, as in the guano-fields of Chile, so large a quantity of nitrates may be formed that they accumulate as an efflorescence on the surface of the soil. This is the mode of origin of Chile saltpetre (potassium nitrate).

The beneficial action of these organisms may be counteracted by the breaking down of nitrates with the evolution of nitrogen by such Bacteria as *Bacterium denitrificans* (*denitrification*). There are, however, others (the *nitrogen-fixing Bacteria*), which actually have the power of fixing the free nitrogen of the air, with the formation of organic nitrogen compounds, although the chemical processes involved are obscure. The most important of the organisms concerned is *Azotobacter* (Fig. 227, *d*), an aerobic form which obtains its energy by the breakdown of carbohydrates, a process setting free a considerable amount of carbon dioxide. The amount of nitrogen fixed is proportional to the amount of organic material decomposed. Another of the nitrogen-fixing Bacteria, *Clostridium pasteurianum* (Fig. 227, *e*), is anaerobic, the principal product of its activity, apart from nitrogenous compounds, being butyric acid. It is the organisms mentioned that are largely responsible for the gradual increase in the nitrogen-content of unmanured grassland. If, however, grasslands contain Leguminous plants, the symbiotic Bacteria (*Bacillus radicicola*, Fig. 227, *f*) present in the root-nodules of the latter are also an important means of nitrogen-enrichment (cf. p. 219).

These different processes are of supreme importance to higher plants and may be briefly epitomised as follows:—



There is thus a continual circulation of nitrogen in nature, and the different organisms concerned evidently work sufficiently well in unison to maintain the balance.[1]

Brief reference may be made to the so-called *Thread-Bacteria*, whose exact relation to the other forms is, however, dubious. In many respects they show a closer approximation to the Blue-green Algæ than to the Bacteria proper. A common form, *Beggiatoa*, which is like a colourless *Oscillatoria*, is frequent in waters rich in sulphuretted hydrogen; the organism in question obtains the energy necessary for the building up of organic substances by the oxidation of the sulphuretted hydrogen to sulphur. The Iron-Bacteria (*Leptothrix*, *Crenothrix*, etc.), whose branched threads are abundant in ferruginous waters, and are often the cause of the brown deposit of ferric hydroxide in moorland streams, are further examples of these forms.

[1] For further details, see S. A. Waksman, *Principles of Soil Microbiology*. Ballière, Tindall & Cox, 2nd edit., 1931 (894 pp.).

CHAPTER XXX

LIVERWORTS AND MOSSES

THE plants so far considered agree in possessing relatively simple sexual organs, consisting of more or less modified single cells, whose contents, with or without division, give rise to the gametes. The sexual organs, moreover, are usually, except in such forms as *Fucus* and *Pelvetia*, distributed over the entire thallus. On the other hand, in Liverworts (Hepaticæ) and Mosses (Musci), which are grouped as *Bryophyta*,[1] the sexual organs are not only much more elaborate, but are commonly restricted to definite portions of the plant-body. The latter also usually exhibits greater cellular differentiation, which may be related to the fact that the majority of the Bryophyta are terrestrial plants and not aquatic like most Algæ.

The majority of Liverworts are damp-loving plants, many of them growing in situations that are covered with moisture in the wetter seasons of the year (*e.g.* along the sides of water-courses), whilst some few are even truly aquatic. Many Mosses, on the other hand, can flourish in habitats that are comparatively dry for a great part of the year, extreme examples being furnished by the Hair Moss (*Polytrichum juniperinum*), found on dry heaths, and the Wall Moss (*Tortula muralis*, Fig. 232, D), common on old walls, rocks, etc.

The body of the Liverwort in its simplest form is a small flat green ribbon-like structure, often repeatedly forked, and growing in close contact with the substratum (e.g. *Metzgeria*, Fig. 228, D, and *Marchantia*, Fig. 228, A). At the base of the notch situated at the tip of each lobe of the thallus lies an apical cell or meristem. The middle part of each lobe is generally somewhat thickened like a *midrib* (Fig. 228), and projects to a more or less marked extent on the lower side of the thallus. Water and nutrient salts are absorbed by numerous fine thin-walled unicellular hairs (*rhizoids*, Fig. 228, A; Fig. 235, A, *r*), which grow out into the soil from the lower surface, often mainly from the region of the midrib; these rhizoids also function as organs of attachment.

[1] For reference-books, see p. 368.

The under side of the thallus, in many Liverworts, also bears one or more rows of flat overlapping *ventral scales* (Fig. 228, E, *v.s.*), which are one cell thick, and not uncommonly purplish in colour. Some (e.g. *Marchantia* and its allies) exhibit, in the axils of these scales, a second type of rhizoid, characterised by possessing a wall with numerous peg-like internal thickenings (Fig. 231, A, B). The capillary channels, between the dense weft of rhizoids and the

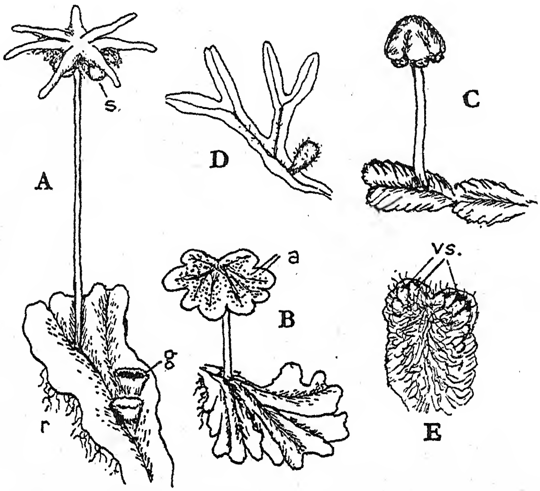


FIG. 228. Thalloid Liverworts. A, *Marchantia*, showing archegoniophore with sporogonia (*s.*), gemma-cups (*g.*), and rhizoids (*r.*). B, Same, with antheridiophore (*a.*). C, *Reboulia*, with archegoniophore. D, *Metzgeria furcata* (under surface). E, Under side of *Preissia*, showing ventral scales (*v.s.*).

overlapping scales, are no doubt of importance in the conduction of water and for its retention during periods of drought.

The Liverworts, however, also include *leafy types* which somewhat resemble Mosses in habit, and, in general, grow in rather drier situations than do the simple thalloid forms; the leaves, unlike those of Mosses, are usually lobed (Fig. 229, A), and sometimes even deeply divided. Two of the commonest genera of foliose Liverworts are *Lophocolea* and *Cephalozia*. Here there is a prostrate stem, bearing on either flank a row of frequently overlapping, sessile, two-lobed leaves (Fig. 229, A) and, on the under side, a row of scales with tufts of rhizoids arising from their base. In some foliose forms the two lobes of the leaves are folded together (e.g. *Scapania*, Fig. 234), and the lower lobe may be modified as a water-receptacle. *Frullania*, a common epiphyte on tree-trunks, affords an extreme example, in which this lobe is developed as a

small, helmet-shaped pitcher (Fig. 230). In the leafy Liverworts, as well as in *Pellia*, the growing point of the stem is invariably a single cell, whereas in *Marchantia* and its allies it consists of a marginal row of cells.

The thallus of most Liverworts exhibits little anatomical differentiation. In *Pellia*, for example, all the cells, apart from their

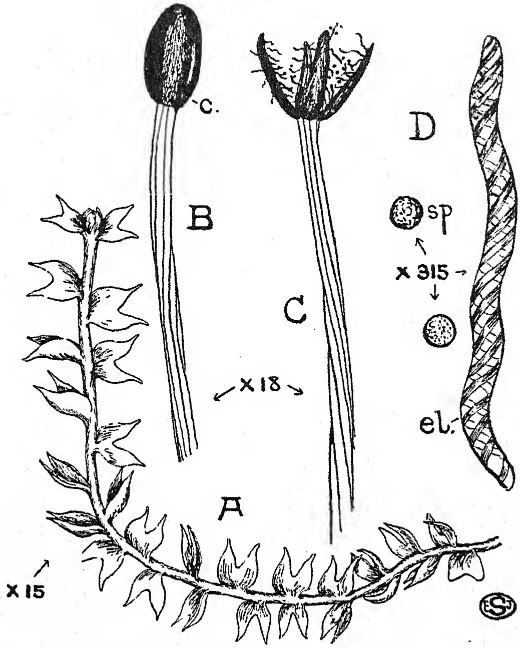


FIG. 229. A Leafy Liverwort (*Cephalozia bicuspidata*). A, Portion of a plant. B, Sporogonium showing capsule (*c.*) before dehiscence. C, The same with dehiscent capsule, showing elaters. D, Elaters (*el.*) and spores (*sp.*).

elongated form in the region of the midrib, are similar in shape, and most of them contain the numerous small discoid chloroplasts which are typical of Bryophyta (Fig. 235, A). An equally simple structure is displayed by most of the foliose forms, the leaves being invariably only one cell thick, and with rare exceptions (e.g. *Diplophyllum*), devoid of a midrib. In *Marchantia* and some of its allies, however, the upper part of the thallus, which is always the principal photosynthetic region, shows considerable complexity (Fig. 231, A). It is subdivided into a large number of very shallow polygonal chambers, each of which is roofed over by an epidermis, and communicates with the exterior through a central

barrel-shaped pore (*p.*). From the floor of each chamber arise numerous short filaments of green cells (*a.*), which form the photosynthetic system of the thallus. The whole of the lower portion of the latter consists of large colourless cells, serving in the main for the storage of food-reserves, and in part showing reticulate thickenings. On the surface of the thallus the photo-

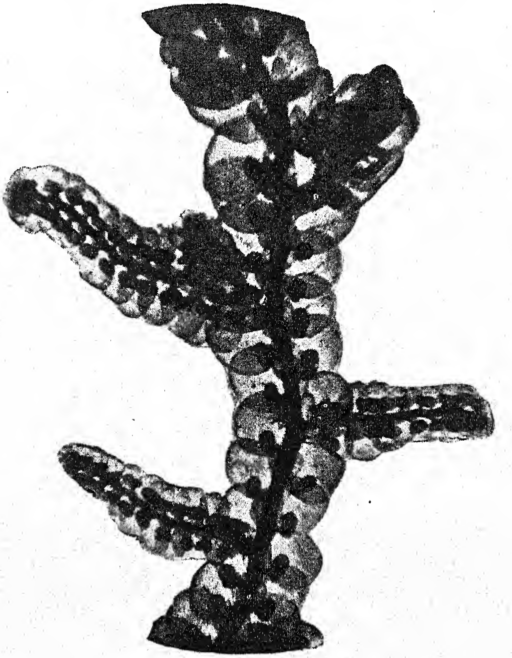


FIG. 230. Photomicrograph of a small portion of the epiphytic Liverwort *Frullania tamarisci*, showing the pitcher-like lower lobes of the leaves. [Photo. E. J. S.]

synthetic chambers appear to the naked eye as a number of small diamond-shaped areas, each with a minute central dot corresponding to the pore.

In the Mosses there is a definite stem usually bearing three or more rows of alternate sessile leaves. The plants either have a prostrate habit (e.g. *Hypnum*, Fig. 232, C), like that of most leafy Liverworts, or grow erect, as in the Hair Mosses (*Polytrichum*, Fig. 232, A, *Funaria*, etc.). The lower part of the stem, which is buried in the soil, forms a kind of rhizome bearing numerous *rhizoids*, and sometimes small scales as well. The rhizoids, which may also develop from the part of the stem just above the soil, are

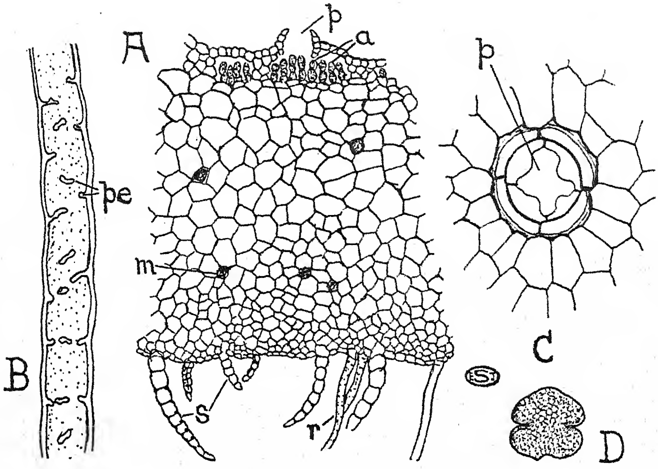


FIG. 231. Structure of *Marchantia*. A, Small part of a transverse section through the thallus. B, Part of a peg-rhizoid, much enlarged, showing the thickenings (*pe.*). C, Surface-view, showing a single pore. D, Gemma, seen from the surface. *a.*, photosynthetic filaments; *m.*, mucilage-cell; *p.*, pores; *r.*, rhizoid; *s.*, ventral scales.

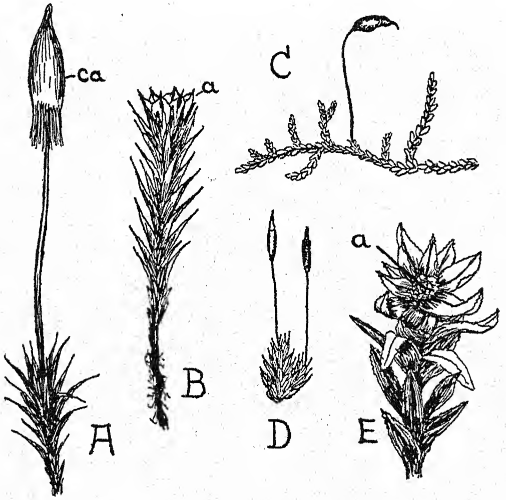


FIG. 232. Various Mosses. A, Plant of *Polytrichum*, bearing a sporogonium whose capsule is covered by the calyptra (*ca.*). B, Male plant of the same, showing the antheridial head (*a.*). C, *Hypnum*, with sporogonium. D, *Tortula muralis*. E, Male plant of *Mnium*, with antheridial head (*a.*).

outgrowths of the superficial cells, but differ from those of Liverworts in being multicellular and branched; they usually have brown membranes, and are divided by oblique septa, just behind which the branches originate.

The leaves of Mosses are never lobed, are attached to the stem by a broad cushion-like base, and usually, except in the region of

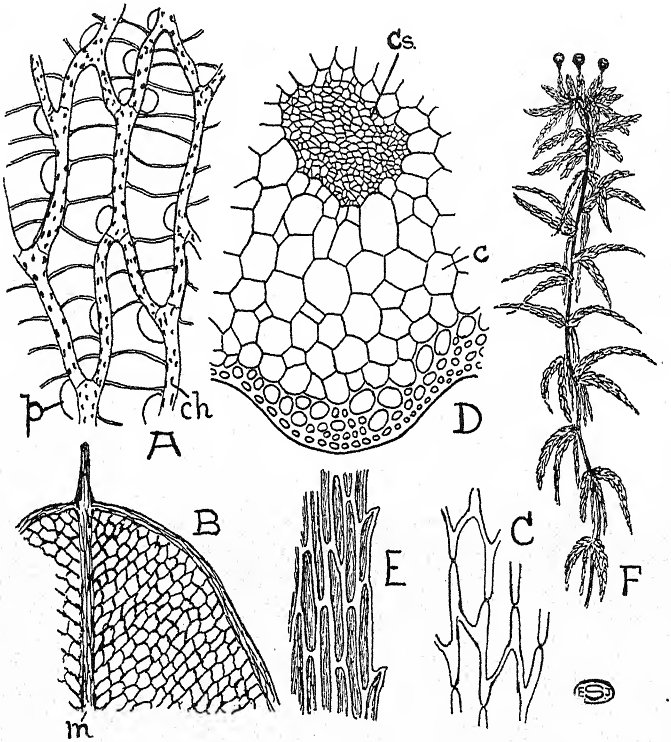


FIG. 233. Structure of Mosses. A, Portion of a leaf of the Bog-moss (*Sphagnum*), showing cells with chloroplasts (*ch.*) and the large empty cells with their thickenings and pores (*p.*). B, Leaf-apex of *Mnium*, with the midrib (*m.*). C, Leaf-cells of *Hypnum*, from the surface, showing thickened walls and pits. D, Transverse section of the stem of *Mnium hornum* (after Bastit), showing conducting strand (*Cs.*) and storage-cells (*c*). E, Leaf-cells of *Hylocomium*, from the surface. F, Habit of *Sphagnum* (after Schimper), showing three sporogonia.

the midrib, consist of a single layer of cells (Fig. 233, B). The midrib (*m.*) is generally well differentiated, and its presence forms a point of contrast with most leafy Liverworts. The branches of the stem arise from below the leaves, and, in some of the erect forms,

are produced in such large numbers from the base that the plants exhibit a densely tufted habit (e.g. *Tortula*, Fig. 232, D). Many of the Bog-mosses (*Sphagnum*) are likewise richly branched. The peculiar habit of these Mosses is partly due to the fact that some of the branches elongate considerably, and hang down alongside the main stem (Fig. 233, F). The branching of many prostrate Mosses takes place in a pinnate manner (e.g. *Hypnum*, Fig. 232, C). Growth of the stem and its branches is effected by means of three-sided apical cells, similar to those of *Equisetum* (cf. p. 51).

Mosses show a greater degree of anatomical complexity than Liverworts, as is well shown by the almost invariable presence in the stem of a distinct *conducting strand*, consisting of small, thin-walled, much elongated cells (Fig. 233, D, *Cs.*); in some of the larger Mosses (e.g. *Polytrichum*) these cells may be of two kinds, perhaps serving respectively for the conduction of water and elaborated food-materials. In Mosses generally conduction of water by capillarity between the leaves and contiguous shoots is also important. The outer tissues of the stem, as seen in transverse section, consist, except in Mosses occupying damp habitats, of cells with strongly thickened walls which are often reddish-brown in colour (Fig. 233, D). Between this peripheral mechanical cylinder and the central conducting strand are larger cells (*c.*) with thinner walls, which seem to function mainly for food-storage.

The cells composing the leaves may be spindle-shaped (as in many species of *Hypnum*, Fig. 233, C), or almost isodiametric (e.g. *Funaria* and *Mnium*, Fig. 233, B), whilst those of the midrib (*m.*), when present, are elongated; the cells at the margin are often produced into teeth, and not uncommonly strongly thickened. The remaining cells may also be somewhat thick-walled, when they frequently bear well-marked pits (e.g. *Hypnum*, Fig. 233, C). In a few Mosses the photosynthetic surface is increased by outgrowths from the stem (e.g. *Thuidium*) or by longitudinal lamellæ, running parallel to the midrib (e.g. *Catharinea undulata*, an abundant Moss in many woods).

The leaves of Bog-mosses (*Sphagnum*) are peculiar in being composed of two kinds of cells (Fig. 233, A). The green photosynthetic cells (*ch.*) are of narrow form, and are arranged as a reticulum whose meshes are occupied by large spirally thickened transparent cells which are dead and empty. The latter communicate with the exterior by means of one or more holes (*p.*) in their walls (cf. the velamen of epiphytic Orchids, p. 111, and *Leucobryum*, p. 523). These large colourless cells readily fill with water, and it is owing to this that so much liquid can be squeezed out of a handful of Bog-moss. Similarly, dry *Sphagnum* can suck up a great deal of

moisture, hence its employment as an absorbent in surgery, or for molasses in the manufacture of Molassine Meal. In the dry condition, the air in the dead cells obscures the green colour of the living ones, and causes the whole plant to appear whitish.

Both Liverworts and Mosses propagate abundantly by vegetative means. In most foliose Liverworts, and some few Mosses, the plant forms special bodies called *gemmæ*, which consist of a varying number of cells and are often of characteristic shape. In *Marchantia* (Fig. 231, D) they are formed in special cup-like outgrowths on the upper surface of the thallus (Fig. 228, A, *g*.), but in the leafy Liverworts they are usually budded off from the tips of the shoots (Fig. 234). An abundant production of gemmæ is likewise seen in the Moss *Aulacomnion androgynum*, where they arise in a spherical cluster at the top of the stem.

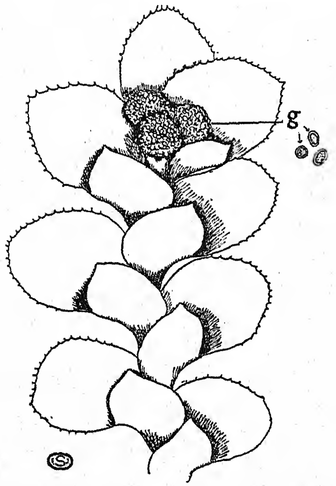


FIG. 234. *Scapania nemorosa*, a Leafy Liverwort, showing gemmæ (*g*) at apex of stem; the same are shown on an enlarged scale at the side.

The ordinary Moss or Liverwort plant, however, also reproduces by sexual means, the *sexual organs* developing especially in the early spring. Their general character, in the Liverworts, will be gathered from an examination of *Pellia*. The male organs are found in the region of the midrib, and are visible to the naked eye as a number of dark pimples, each of which, in a vertical section (Fig. 235, A), is seen to correspond to a single more or less spherical *antheridium*. The latter (Fig. 235, B) is borne on a very short stalk, and almost fills a flask-shaped cavity in the thallus which communicates with the exterior by a narrow pore.

The antheridium is a multicellular structure with a wall (Fig. 235, B, *w*.) of a single layer of cells containing chloroplasts and, at maturity, encloses numerous small, colourless, closely packed *spermatozoid mother-cells*, each producing a single spermatozoid (Fig. 235, D). Through vigorous absorption of water the apex of the antheridium is ruptured, and the expanding mucilaginous mass of mother-cells is discharged into the surrounding moisture. Here occurs the final liberation of the *spermatozoids*, each of which possesses a spirally coiled body (formed mainly from the nucleus

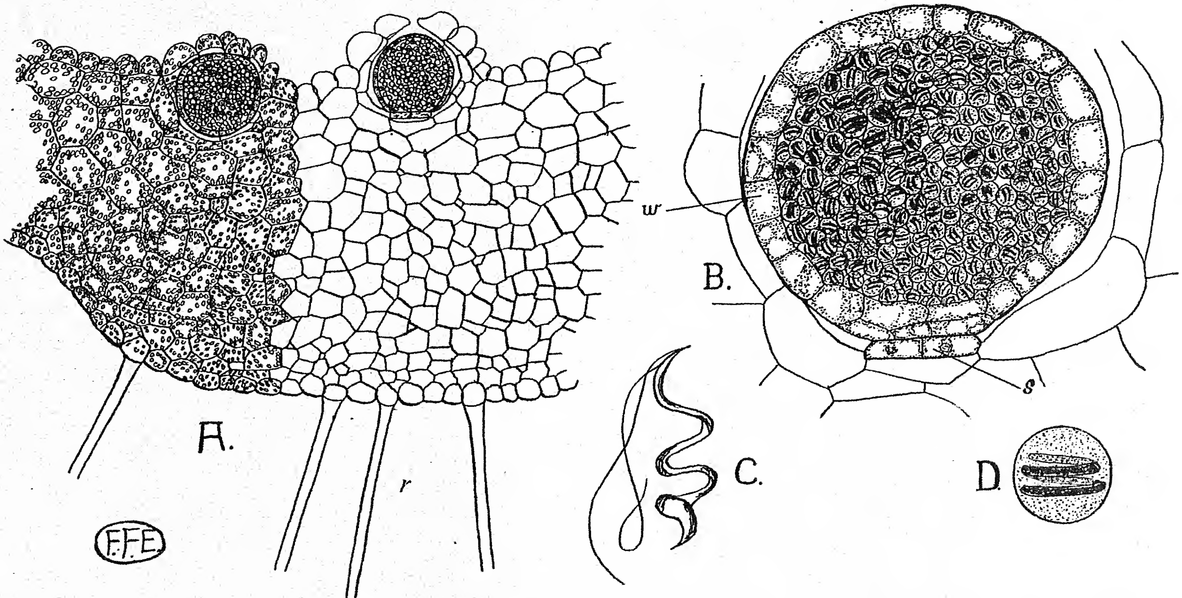


FIG. 235. A, Part of a transverse section through the thallus of *Pellia*, showing the numerous small chloroplasts in the cells (only indicated in part of the figure), the rhizoids (*r.*), and two antheridia within their respective cavities, that on the right showing the aperture to the exterior. B, A single antheridium, much enlarged, showing the short stalk (*s.*), the wall (*w.*), and the numerous mother-cells in which the spermatozoids are seen in course of development. C, A single spermatozoid. D, A spermatozoid mother-cell enlarged, with the contained spermatozoid. (C, after Guignard, the rest original.)

of the mother-cell), bearing two long flagella at the slightly tapering front end (Fig. 235, C).

A rather exceptional grouping of the antheridia obtains in *Marchantia*, where the stalked thallus-lobe, in which the male organs are sunk, is raised above the general surface (Fig. 228, B). Amongst the leafy forms the antheridia are situated, either singly or in groups, in the axils of the leaves.

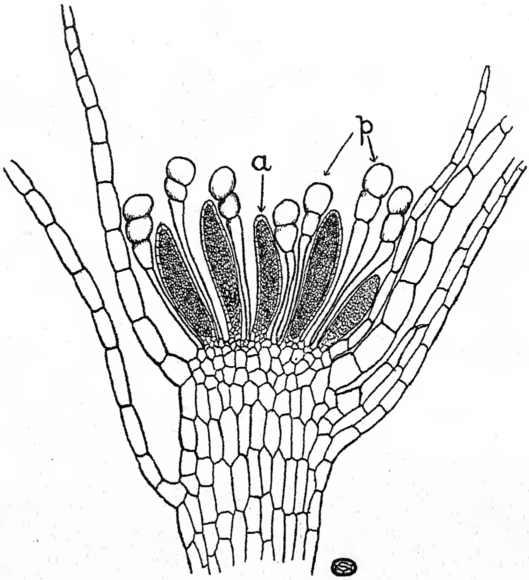


FIG. 236. Vertical section through the antheridial head of the Moss *Funaria*, showing the antheridia (*a.*) and interspersed sterile hairs (*p.*).

The antheridia of Mosses show essentially the same structure as those of Liverworts, except that they are elongated and possess a broader stalk (Fig. 236, *a.*). They occur in groups, interspersed with multicellular sterile hairs (*p.*), at the top of the stem or its branches. Each antheridial group is surrounded by a number of spreading protective leaves (*involucre*), which are not infrequently arranged to form a kind of cup, and usually differ in shape and size, and sometimes also in colour, from the ordinary leaves. The male plants of Mosses are thus easily recognised (Fig. 232, B, E). The spermatozoids are like those of Liverworts, and are liberated in the same way, the mass of mother-cells often being ejected to some slight distance.

The female organs, or *archegonia*, which are essentially similar

in the two groups, differ markedly from those of Thallophyta. They are flask-shaped structures (Fig. 237, B), composed of a lower swollen part, or *venter* (*v.*), and a long neck (*n.*), which, in Mosses, is often twisted. The neck is a tube consisting of a single layer of elongated cells arranged in five or six longitudinal rows and surrounding a narrow canal. The latter is occupied by a row of naked *neck-canal cells* which ultimately become mucilaginous, and, in swelling, push apart four lid-cells which, till then, close the upper end of the neck-canal. The venter possesses a wall (one-layered in Liverworts, Fig. 237, B, two-layered in Mosses), enclosing

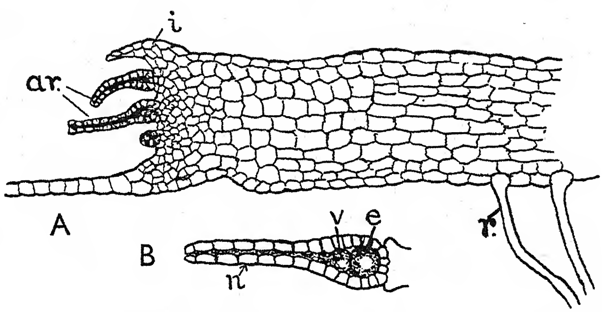


FIG. 237. A, Longitudinal section through the apex of the thallus of *Pellia*, showing a group of archegonia (*ar.*) and the involucre (*i.*). *r.*, rhizoid. B, Single archegonium of *Marchantia*, on a larger scale. *e.*, egg; *n.*, neck; *v.*, ventral canal cell.

a large naked *ovum* (*e.*), with a small *ventral canal cell* (*v.*) at the base of the neck. The venter is borne on a short stalk which is rather more massive in Mosses than in Liverworts.

In Mosses, where they are interspersed with sterile hairs, and in most leafy Liverworts, the archegonia occur in groups at the top of the stem or its branches. They are enveloped by a number of "*involucral*" leaves which generally differ in size, and sometimes also in shape and colour, from the ordinary leaves; in most Mosses, however, such archegonial groups are scarcely distinguishable from the ordinary leaf-buds. In some leafy Liverworts (e.g. *Lophocolea*) the leaves of the involucre are fused together, almost to their tips, to form a cup.

In some of the thalloid Liverworts (e.g. *Pellia*) the archegonia are found at the front end of the thallus, where they occupy depressions roofed over by a scale-like involucre (Fig. 237, A, *i.*). In others (e.g. *Marchantia*, Fig. 228, A) and *Reboulia* (Fig. 228, C) they are situated on special upgrowths which are divided into 4–10 lobes or branches; the archegonia form groups on the lower surface,

between the lobes, each group being enclosed between a pair of involucral scales.

The diverse forms of involucre surrounding the archegonia not only protect them from desiccation, but form capillary chambers tending to retain water. This facilitates the movement of the sperms in fertilisation, which only takes place when the plant is covered with a film of moisture. In forms like *Marchantia*, the stalk bearing the lobed archegonial disc does not lengthen till after fertilisation, so that the necks of the archegonia remain in close contact with the water-film on the upper surface of the thallus. In the same way the branches bearing the archegonial groups of Mosses are at first usually short and adjacent to the soil, so that they are readily covered with moisture.

After escaping from the antheridia, the spermatozoids, swimming in the surface films of moisture, are chemotactically attracted to the open necks of the archegonia by substances (cane-sugar in Mosses) contained in the mucilage formed by the breaking down of the canal cells. The spermatozoid passes down the neck-canal and enters the egg, after which nuclear fusion occurs and a diploid condition (p. 314) is established.

The fertilised ovum or zygote secretes a cell-wall and, without any resting-stage, grows into a new plant. This, however, in both groups differs fundamentally from the parent, especially in being parasitic upon the latter, and at maturity constitutes an organism (the *sporogonium*, Fig. 232, A; Fig. 238, A) that is almost solely concerned in the production and dispersal of spores. This simplicity of structure can possibly be related to the parasitic habit, thus affording an interesting analogy to parasitic Flowering Plants. As the embryo enlarges, the venter of the archegonium stretches and grows into a protective covering, the *calyptra*, which can often be recognised around the young sporogonium (Fig. 238, B, C; and Fig. 239, I, *c*.).

In Liverworts the dividing ovum first forms a spherical mass of cells which later elongates and gradually becomes differentiated into three regions. The end adjacent to the thallus penetrates into the underlying tissue as a cone-shaped sucker, the *foot* (Fig. 238, B, *f*.). This consists of parenchymatous cells, and serves to absorb and transfer food to the developing sporogonium. The opposite end swells into a, usually, spherical *capsule* (*ca*.) with a wall of one or more layers enclosing a mass (the *archesporium*) of spore-forming cells. Up to a certain stage all the latter are alike, but the archesporium in most Liverworts ultimately differentiates into two kinds of cells, which at first are often arranged in radiating series. One type is rounded, and, since each of these

cells divides to form four spores (Fig. 238, C, *sp.*), they are known as *spore mother-cells*. The first division in the spore mother-cell is the reduction division (p. 314). The other cells are elongated and

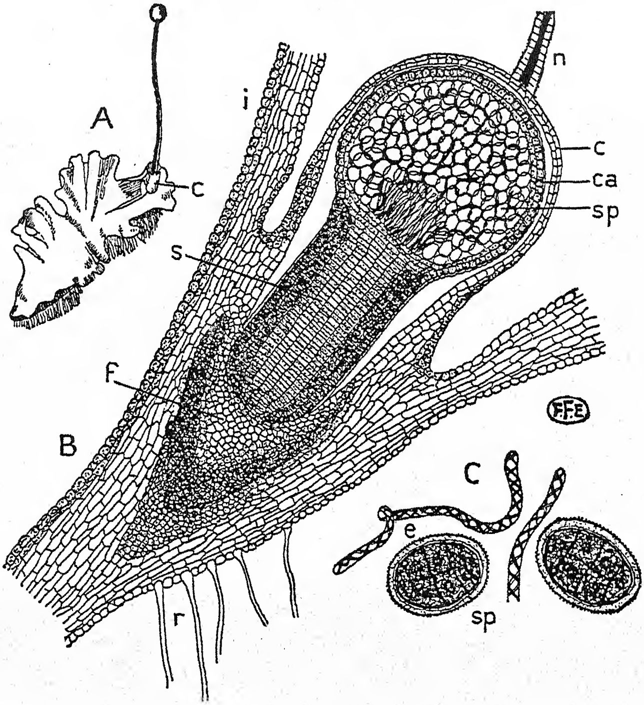


FIG. 238. The sporogonium of *Pellia*. A, Small part of a thallus, showing a mature sporogonium, with the ruptured calyptra (*c.*) at the base (after Leunis). B, Longitudinal section through an almost mature sporogonium, still enclosed within the calyptra (*c.*); the elaters are shown as dark lines among the much larger spores. *ca.*, wall of capsule; *f.*, foot; *i.*, involucre; *n.*, neck of archegonium; *r.*, rhizoid; *s.*, seta; *sp.*, spore. C, A group of spores (*sp.*) and elaters (*e.*).

at first thin-walled, when they assist in the translocation of food-materials to the developing spores, but subsequently they acquire spiral thickening bands, and form so-called *elaters* (Fig. 238, C, *e.*; see also Fig. 229, D).

The region between capsule and foot, consisting of small cells, often densely crowded with starch-grains, constitutes the *seta* or *stalk* (Fig. 238, B, *s.*), which always remains short until the spores are mature At this stage, however, in *Pellia* and most leafy Liverworts, the stalk elongates rapidly, owing to a great increase

in the length of its cells at the expense of the starch-reserves, and bursts through the calyptra, which can be recognised as a torn sheath around its base (Fig. 238, A, *c.*). The capsule is thus raised above the damp soil into the less humid air, where dispersal of the spores by air-currents is more readily attained. Where, as in *Marchantia*, the archegonia are borne on a special receptacle, the stalk of the latter elongates after fertilisation (cf. above), and serves the same purpose as the seta of other Liverworts, whilst the sporogonium retains the short stalk of the embryonic phase (Fig. 228, A, C).

In *Pellia* and most leafy Liverworts the capsule-wall splits into four petal-like valves (Fig. 229, C), although in *Marchantia* the apex ruptures irregularly. Owing to their unequal thickening, the elaters tend to coil and bend as the contents of the capsule become drier. This movement is, however, prevented by the tightly packed contents until rupture of the capsule takes place, when the tensions set up in the elaters are manifested in a wriggling movement which loosens the mass of spores and flicks them into the air. Not uncommonly tufts of elaters remain adhering to the top of the stalk (e.g. *Pellia*) or to the valves (Fig. 229, C).

In Mosses the embryo elongates considerably at an early stage, and soon acquires the shape of a rod tapering at either end (Fig. 239, H and I). The lower extremity penetrates into the tissue of the Moss-stem and forms the absorptive *foot* (*f.*), which is, however, much less clearly distinguished than in Liverworts. Soon, a swelling, the *apophysis*, appears on the rod-shaped embryo, a little way above its middle, separating the future seta and capsule. The apophysis, which plays a part in the nutrition of the growing sporogonium, is a local photosynthetic region composed of cells rich in chloroplasts and provided with abundant intercellular spaces (Fig. 239, A, *ap.*). The epidermis here contains *stomata* (Fig. 239, F) like those of higher plants, except that in many Mosses the septa between the guard-cells break down at maturity, so that the latter form an oval canal surrounding the pore (Fig. 239, G).

The upper part of the embryo enlarges progressively, during the subsequent development, to form the capsule, so that at maturity the latter is usually far more prominent than the apophysis, which, though it always remains recognisable, does not grow much after its first formation (cf. Fig. 239, A). The mature capsule is here also raised aloft by a considerable elongation of the slender *stalk* (Fig. 232), and again this causes rupture of the calyptra. In Mosses, however, this takes place in such a way that the upper part of the calyptra is carried up on the capsule as a hood (Fig. 232, A, *ca.*). When this is removed, the apex of the capsule is seen to

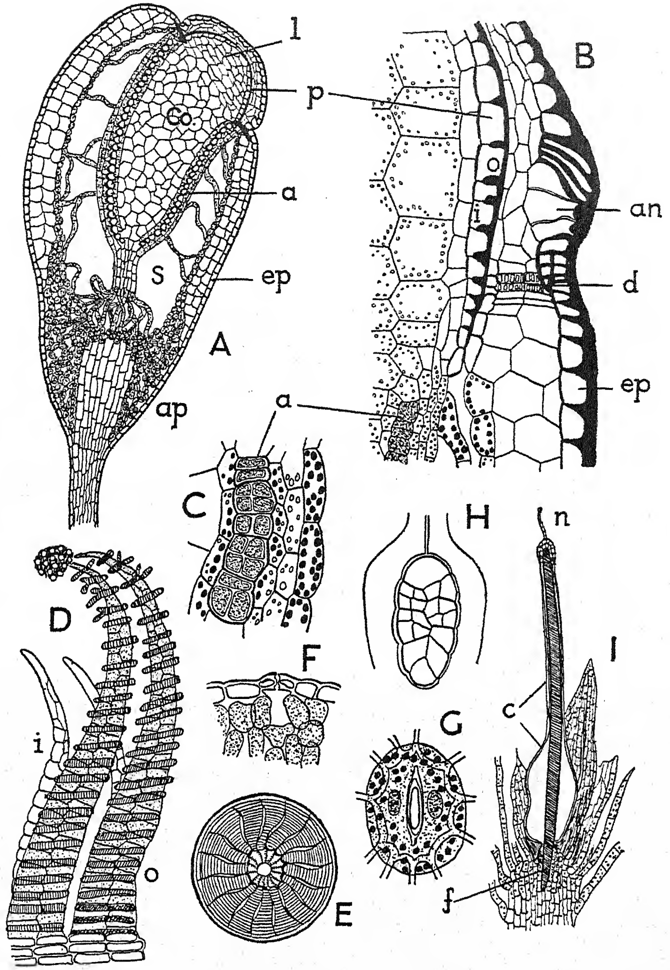


FIG. 239. Structure and development of the Moss-sporogonium (all figures, except F, represent *Funaria hygrometrica*). A, Longitudinal section through young capsule, apophysis (*ap.*), and the top of the stalk. B, Part of the capsule in the region of the lid, much enlarged. C, Small part of archesporium and spore sack, enlarged. D, Two pairs of peristome-teeth (inner and outer). E, Aperture of dehisced capsule, showing arrangement of peristome-teeth. F, Section of small part of apophysis of *Bryum argenteum*, showing stoma. G, Single stoma, in surface-view. H and I, Stages in development of the sporogonium. *a.*, archesporium; *an.*, annulus; *c.*, calyptra; *Co.*, columella; *d.*, diaphragm; *ep.*, epidermis; *f.*, foot; *i.*, inner peristome tooth; *l.*, lid; *n.*, neck of archegonium; *o.*, outer peristome tooth; *p.*, peristome-layer; *S.*, air-space. (D, after Ruhland; E, after Braithwaite; F and G, after Haberlandt; the remainder after Sachs.)

be separated from the rest by a slight constriction, and it is this part that becomes detached as a *lid* and allows of dispersal of the spores.

The internal structure is best studied in a longitudinal section of a nearly ripe capsule (Fig. 239, A). Here the axis is occupied by a rather broad column of thin-walled parenchyma (the *columella, Co.*) passing below into the tissue of the apophysis (*ap.*) and above into that of the lid (*l.*). Surrounding the columella are two concentric cylinders of cells, separated by the granular *archesporium* (*a.*), each mother-cell of which, as in Liverworts, divides to form four spores (Fig. 239, C). Between the spore-sack so formed and the capsule-wall is a conspicuous air-space (*S.*) bridged by occasional fine threads of green cells; in a few Mosses (e.g. *Polytrichum*) a similar air-space separates the spore-sack from the columella. The capsule is protected by a thick-walled epidermis (*ep.*) beneath which are several layers of cells containing chloroplasts. The features just described are equally recognisable in a transverse section through the middle of the capsule.

Just below the constriction (Fig. 239, A and B) marking the commencement of the *lid*, a diaphragm (*d.*) composed of thickened cells, and having the form of a circular ledge perforated by the central thin-walled tissue, stretches inwards from the epidermis (*ep.*) of the capsule. Arising from the inner edge of this diaphragm is a dome-shaped layer of cells (the *peristome, p.*) characterised by marked thickening of the outer tangential walls (*o.*) and of the adjoining portions of the horizontal walls, although the radial (*i.e.* vertical) walls remain thin. At the lower edge of the lid the thick-walled epidermis is interrupted by one or two rings of larger thin-walled cells which constitute the so-called *annulus* (*an.*). Dehiscence eventually takes place along this line, as a result of the differential shrinkage between the annulus and the adjacent cells; soon after the lid is blown away. The epidermal cells above the annulus are usually markedly flattened, and form the lower edge of the lid (Fig. 239, B).

At maturity all the thin-walled tissues of the capsule shrivel, leaving, apart from the spores, only the epidermis, the diaphragm, and the thickened walls of the peristome. Each of the rows of cells forming the latter necessarily tapers from base to apex, and, as a result of the breaking down of the thin radial (*i.e.* vertical) walls between some or all of the rows, a number of separate plate-like *peristome-teeth* (Fig. 239, D), attached below to the edge of the diaphragm, are formed. Sometimes both inner and outer tangential walls of the peristome are thickened, when a double set of teeth (*o.* and *i.*) of course arises as the thin portions of the horizontal

walls shrivel. The peristome varies greatly in different Mosses, and, together with the characters of the leaves, constitutes one of the chief means for distinguishing the different genera and species.

The peristome-teeth are extremely sensitive to changes in the moisture-content of the air, curling outwards when the latter is dry, and inwards when it is damp. This is due to differential expansion or contraction on the two sides of each tooth depending on the unequal distribution of thickening. In dry weather, therefore, the powdery mass of spores inside the capsule is readily dispersed, whilst in wet weather the dome is reconstituted (Fig. 239, E), and the aperture, left by the shedding of the lid, closed. The actual dispersal, in which the elasticity of the seta plays a considerable part, is effected by a catapult-mechanism similar to that of some fruits (cf. p. 480).

In *Sphagnum* the sporogonium (Fig. 233, F) is a short structure without a stalk, like that of *Marchantia*, but here there is a definite lid and a dome-shaped archesporium. The apparent stalk is a prolongation of the apex of the leafy stem which develops after fertilisation (cf. *Marchantia*), and in the top of which the foot is embedded.

The spores ultimately give rise to a new Liverwort or Moss, but the adult plant is not produced directly on germination. This is especially obvious in Mosses, where the spores usually develop into a branched multicellular filamentous structure, the *protonema*, which exists partly above and partly below ground (Fig. 240, C). The overground portion appears as a green weft on the surface of the soil, and its cells contain numerous discoid chloroplasts (Fig. 240, D), whilst the underground portion closely resembles the rhizoids of the ordinary Moss (Fig. 240, C, *r.*). In fact, the latter readily grow out into protonema, if exposed to the light, and can thus bring about the development of new plants. Vegetative multiplication of the protonema, by the detachment of branches or of small terminal groups of cells (Fig. 240, C, *g.*), is often prolific, and may set in at a comparatively early stage.

Sooner or later some of the short lateral branches of the protonema become pear-shaped and undergo segmentation by three oblique walls to cut out the characteristic tetrahedral apical cell of the stem of the adult Moss (Fig. 240, A, *b.*). By its continued divisions a small mass of cells is formed from which leaves soon arise, and it is not long before the new Moss attains recognisable dimensions. This formation of Moss-plants takes place at many points on the protonema, and, as the latter usually dies away soon after, the individuals become independent. A protonema readily develops from most parts of the adult Moss, in fact, whenever vegetative propagation from fragments of the plant occurs (cf. p. 358), a

protonema is first formed, and from this the new plants arise secondarily.

The protonema of the foliose Liverworts is similar in appearance to that of Mosses, but in most of the thalloid species the early stages are not sharply marked off from the adult.

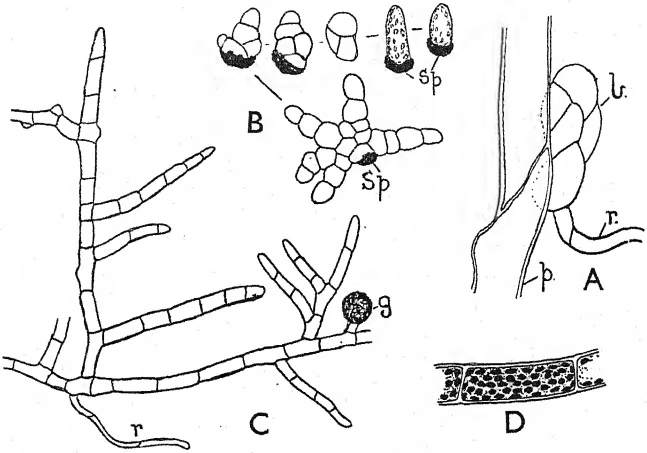


FIG. 240. Moss-protonema. A, Development of young *Funaria*-plant (*b*) from the protonema (*p.*) (after Campbell). B, Stages in germination of spores, and C, Protonema of *Dicranella heteromella* (after Servettaz). *g.*, gemma on protonema; *r.*, rhizoids; *sp.*, spore-membrane. D, Single cell of overground part of protonema.

The life-history of the Bryophyta thus includes two distinct phases: the one, concerned in the production of the sexual organs, is usually highly specialised morphologically and self-supporting, whilst the other, concerned solely with the production of asexual spores, is always dependent, and relies for its sustenance, either entirely (most Liverworts) or partly (Mosses), upon food obtained from its host. These two phases normally alternate with one another and arise from one another, and an analogous alternation is encountered in all the higher groups of plants. For convenience of designation the diploid spore-producing phase is spoken of as the *sporophyte*, and the haploid sexual phase as the *gametophyte*.

[For a more detailed treatment of Bryophyta, see F. Cavers, "The Interrelationships of the Bryophyta," *New Phytologist*, vols. 9–10, 1910–11; and F. Verdoorn *et al.*, *Manual of Bryology*, The Hague, 1932 (486 pp.). For taxonomic works, see p. 579.]

CHAPTER XXXI

FERNS (FILICALES)

THE Bryophyta, though exhibiting a marked advance in organisation as compared with the Thallophyta, differ from the remaining flowerless plants, or *Pteridophyta*, in lacking roots and specialised conducting tissue. In the Pteridophyta the gametophyte is usually thalloid and short-lived, whilst the sporophyte is far more conspicuous and more permanent, and is quite independent of the gametophyte except in its earliest stages. In the sexual process and the general structure of the sexual organs, however, there is considerable resemblance between the two classes. Pteridophyta, like Bryophyta, possess motile male cells, and thus depend on the presence of liquid water at the time of fertilisation. The former generally grow in moist habitats, although quite a considerable number tolerate relatively dry conditions. Included in the Pteridophyta are the Ferns (Filicales), the Horsetails (Equisetales), and the Clubmosses (Lycopodiales).

In many common Ferns[1] the stem is relatively insignificant in comparison with the conspicuous, usually deeply divided, pinnate fronds. The Tree Ferns of subtropical regions, however, have well-marked trunks. The stem is either a rhizome (as in the Bracken, *Pteridium aquilinum*, Fig. 241, B), or compact and more or less erect (*e.g.* Royal Fern, *Osmunda regalis*). It rarely shows branching, though this occurs at intervals where the rhizome is elongated (*e.g.* Bracken). In the prostrate types, the leaves usually arise in rows on either side of the underground stem, and are separated by well-marked internodes (Fig. 241, B). In short-stemmed species, however, whether the root-stock be erect or inclined (*e.g.* Male Fern, *Nephrodium filix-mas*), the leaves are densely crowded, and show an obvious spiral arrangement. Adhering bases of the leaves, which persist after lamina and petiole have died away, add appreciably to the apparent thickness of the stem. All the *roots* of the adult Fern are adventitious (Fig. 241, B); they usually arise in the neighbourhood of the leaf-bases, and are generally black in colour and forked.

[1] For reference-books, see p. 385.

The young *leaf* is commonly more or less densely clothed with brown scaly hairs or *ramenta*, many of which are shed as the blade unfolds; they usually persist, however, upon the petioles (Fig. 242, A, *r.*) and on the leaf-bases. As the leaf-rudiment produced behind the growing point gradually develops, the axis of the lamina becomes coiled after the manner of a watch-spring, and, in compound leaves,

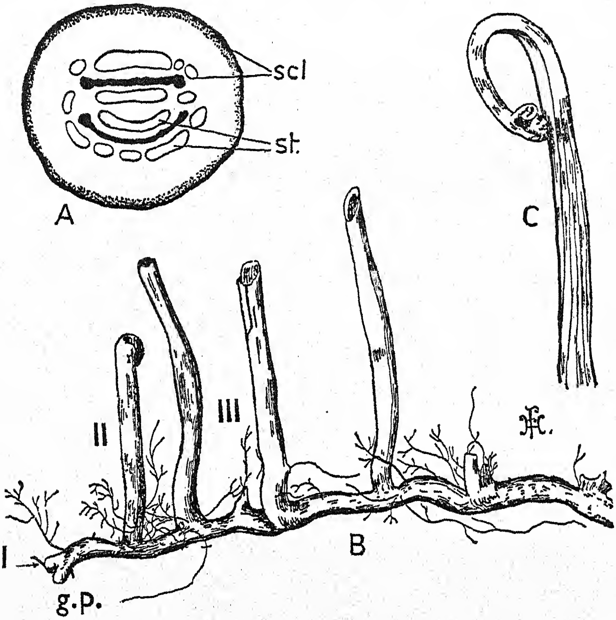


FIG. 241. The Bracken (*Pteridium aquilinum*). A, Diagram of transverse section of rhizome. *scl.*, sclerenchyma; *st.*, steles. B, Rhizome showing apex with growing point (*g.p.*), successively older leaves (I, II, III), and the bases of leaves of former seasons. *C*, Young frond.

the individual portions become inrolled in a similar way (*circinate vernation*) (Fig. 241, C). Each segment of the blade grows by means of an apical cell, which thus occupies a protected position within the spiral formed by the maturer parts. These features are readily observed in a young Bracken-frond, as it emerges from the soil, and the prolonged growth of its tip is evidenced by the retention of the coiled character in the uppermost portion, long after the older basal portion is fully expanded. The development of Fern-leaves is usually very slow, the rudiment being produced and undergoing gradual enlargement for two or more years before the frond appears above the surface (cf. Fig. 241, B, I, II, III).

Not all Fern-leaves are as deeply compound as in the Bracken or

Lady Fern (*Athyrium filix-fœmina*). Those of the Polypody (*Polypodium vulgare*, Fig. 242, B) and Hard Fern (*Blechnum spicant*, Fig. 248), for instance, are simply pinnate, whilst those of the Hart's Tongue Fern (*Scolopendrium vulgare*, Fig. 242, A) are undivided. The venation is exceedingly characteristic, the midribs of the leaves or pinnæ, as the case may be, bearing numerous forked lateral veins which are often not connected by cross-branches (Fig. 246, A, B).

A general idea of the more characteristic features in the internal *structure of the stem* can be gathered from a study of the Bracken rhizome. In transverse section (Fig. 241, A) this is seen to be traversed by two rings of vascular strands or *steles* (*st.*). Separating the rings are two bands of dark brown sclerenchyma (*scl.*), and the same tissue also forms a layer beneath the epidermis; its elements (Fig. 244, *Scl.*) differ from the fibres of higher plants in being short and relatively thin-walled. The remaining ground tissue is parenchymatous, and contains an abundance of starch.

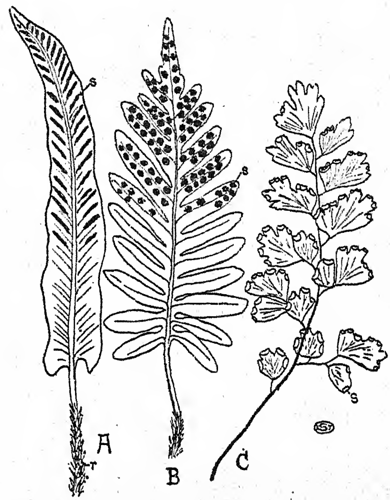


FIG. 242. Entire fronds of A, Hart's Tongue Fern (*Scolopendrium vulgare*); B, Polypody (*Polypodium vulgare*); and C, Maidenhair Fern (*Adiantum*). *r.*, ramenta; *s.*, sori. (All three considerably reduced.)

The vascular strands are concentric (Fig. 243), with the component tissues more or less symmetrically arranged. The term stele is customarily applied to these concentric strands of Ferns, but this does not necessarily imply that they are comparable to the entire vascular cylinder of a higher plant. Each stele is bounded by an endodermis (*En.*), with dark brown membranes, and a pericycle (*P.*), composed of rather larger thin-walled cells. Next follow one or two layers of much smaller cells, constituting the so-called phloem-parenchyma (*P.p.*). Immediately within is a conspicuous zone consisting chiefly of large, empty-looking, thin-walled elements, the sieve-tubes (*S.*), which are often absent towards the ends of the strands, and which are separated from the central xylem by a zone of small-celled wood-parenchyma (*X.p.*). The bulk of the xylem consists of large tracheids (*Xy.*), but near the ends and towards the centre of the strand, small

elements, representing the protoxylem (*P.xy.*), can usually be

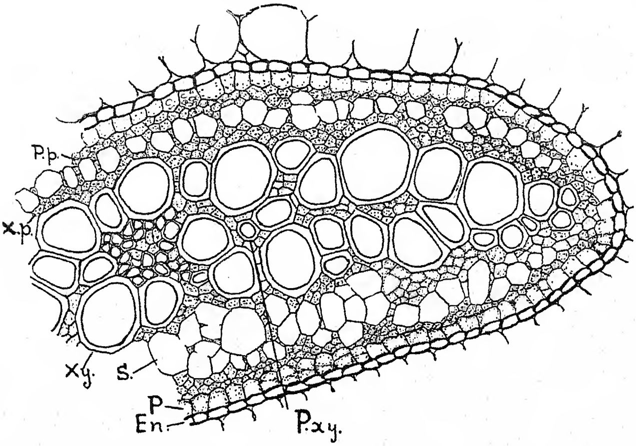


FIG. 243. Part of a stele from the rhizome of the Bracken (*Pteridium aquilinum*), in transverse section. *En.*, endodermis; *P.*, pericycle; *P.p.*, phloem-parenchyma; *P.xy.*, protoxylem; *S.*, sieve-tube; *X.p.*, xylem-parenchyma; *Xy.*, xylem.

recognised. There is generally a small central mass of wood-parenchyma.

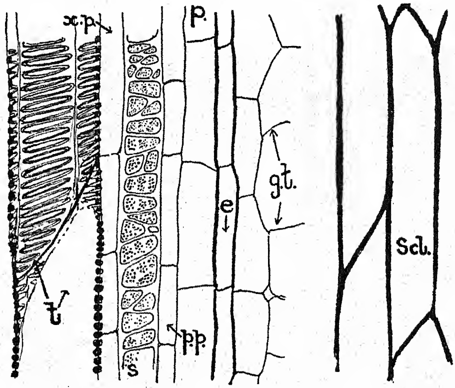


FIG. 244. On the left, part of a radial longitudinal section through one of the steles of the Bracken-rhizome. *e.*, endodermis; *g.t.*, ground tissue; *p.*, pericycle; *p.p.*, phloem-parenchyma; *s.*, sieve-tube; *t.*, tracheid of the metaxylem; *x.p.*, xylem-parenchyma. On the right, a little of the sclerenchyma (*Scl.*) in longitudinal section.

In longitudinal sections, cut so as to pass radially through a stele (Fig. 244), the *sieve-tubes* appear as elongated structures with tapering ends, and bearing the sieve areas on their sloping radial

faces. Under the high power these sieve areas exhibit a rather irregular thickening of shining bars (*s.*), with intervening darker zones exhibiting a fine dotting and bearing a number of highly refractive adhering granules. The longitudinal walls of the meta-xylem *tracheids* (*t.*) exhibit several rows of closely arranged oblong bordered pits, producing an exceedingly characteristic type of

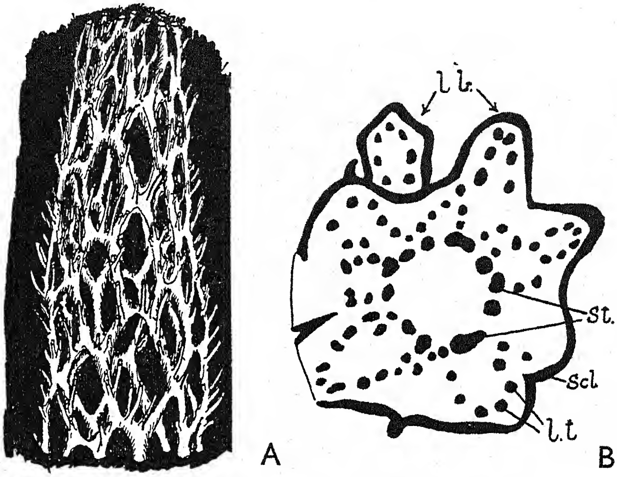


FIG. 245. *Nephrodium filix-mas.* A, Skeleton of vascular system showing the cylindrical network of steles, with numerous leaf-trace strands arising from the edges of the "leaf-gaps" (original). B, Transverse section of the rhizome (after De Bary). *l.b.*, leaf-bases; *l.t.*, leaf-trace strands; *Scl.*, sclerenchyma; *St.*, stem-steles.

scalariform thickening, whilst the protoxylem tracheids are spirally thickened in the usual way.

The number of steles observed in a transverse section of the stem varies considerably in different Ferns. Some (e.g. *Gleichenia*, common in the Tropics) possess but a single central stele of comparatively large size, whilst some of the Tree Ferns exhibit a complex system of several concentric rings of steles. In the Male Fern, again, the strands form but a single ring (Fig. 245, B, *St.*). The arrangement and histological structure of the vascular tissues within each stele is, however, essentially the same in all. The young Fern seedling always possesses but a single central strand which, as the plants become older, enlarges and, in forms like *Nephrodium* and *Pteridium*, gradually separates into the distinct steles of the adult.

The relations between the vascular system of stem and leaf

are easily recognised in *Nephrodium* when the rhizome has been allowed to rot, so that all but the hard vascular tissues have disintegrated. In the resulting skeleton (Fig. 245, A) the steles form a cylindrical network, in which each mesh or *leaf-gap* corresponds in position to the attachment of a leaf. The latter is supplied by the numerous fine strands passing through the cortex from the margin of the mesh. These *leaf-traces* can be recognised, in a transverse section of the rhizome (Fig. 245, B), as arcs of small strands (*l.t.*) occupying the lobes that represent the leaf-bases (*l.b.*). In *Pteridium* a series of transverse sections, cut in the region of the node, shows that the leaf-base is supplied by several strands passing off from the outer ring. The gap thereby created is filled by steles from the inner series, which pass out, through a break in the sclerenchyma-ring, and also supply strands to the petiole. The petiole in both these Ferns is thus traversed by a large number of strands, normally forming an arch, but in certain genera (e.g. *Gleichenia*) the leaf-stalk, like the stem, contains but a single stele.

The structure of the *leaf* conforms to the dorsiventral type. Since many Ferns grow in shady situations, the epidermis often contains chloroplasts, and the palisade tissue is not uncommonly poorly developed or the mesophyll may even be spongy throughout (cf. Fig. 250). The ultimate branches of the concentric strands traversing the petioles become collateral within the pinnæ, owing to development of the phloem only on the lower side.

The *roots* of most Ferns are diarch, and owe their frequent wiry character to the development of an exceedingly thick-walled sclerenchymatous cortex, but otherwise do not differ appreciably from those of other plants. The tetrahedral apical cell, by whose divisions the tissues of stem and root are formed, has already been described on p. 51.

The Fern-plant sooner or later commences to produce spores. These are developed within small, stalked, usually brown-coloured *sporangia*, almost invariably borne on the under-surfaces of the fronds. Most commonly they are arranged in numerous separate groups, or *sori*, each usually comprising a considerable number of sporangia arising from a slight central swelling of the leaf-tissue, known as the *placenta* (Fig. 250, *pl.*).

Such sori are well seen in the Common Polypody (*Polypodium vulgare*, Fig. 242, B, *s.*), where they appear as small circular brown patches situated over the lateral veins of the pinnæ. A similar arrangement obtains in *Nephrodium* (Fig. 246, B), but here each sorus is protected by a kidney-shaped outgrowth (*indusium*, *In.*) of the placenta, which withers when the sporangia are mature. In the Maidenhair Fern (*Adiantum*, Fig. 242, C, *s.*) and the Wall

Rue (*Asplenium ruta-muraria*) the sori are near the edges of the pinnules; in the latter they are covered by indusia having the form of little flaps projecting inwards from the margin (Fig. 246, C). In *Pteridium* (D), where the sporangia form a continuous fringe all round the margin of the pinnule, the incurved edge of the latter functions as an indusium.

A peculiar type of sorus is found in the Filmy Ferns (Hymenophyllaceæ), which are so called because of their delicate fronds,

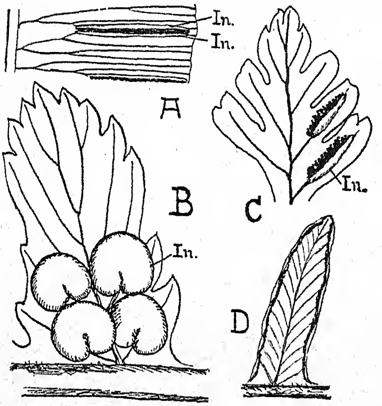


FIG. 246. Sori of various Ferns. A, Hart's Tongue Fern (*Scolopendrium*). B, Male Fern (*Nephrodium*). C, *Asplenium*. D, Bracken (*Pteridium*). *In.*, indusium.

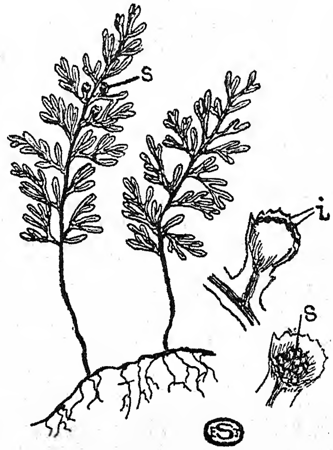


FIG. 247. On the left part of a Filmy Fern (*Hymenophyllum tunbridgense*), bearing sori (*s.*). The two smaller figures on the right show a sorus, entire and in longitudinal section respectively. *i.*, indusium; *s.*, sorus.

consisting of but a single layer of cells. Though mainly encountered in the Tropics, they are represented in Britain by one or two species (e.g. *Hymenophyllum tunbridgense*, Fig. 247) occurring in damp caves and other humid situations in rocky districts. Here the sporangia arise in sequence from above downwards on rod-like placentæ (*s.*) projecting from the leaf-margin, and each sorus is enveloped at its base in a cup-shaped indusium.

In most Ferns there is only one kind of frond which fulfils the ordinary functions of a leaf, as well as those connected with spore-production. In a few species, however, there is division of labour, as in the Hard Fern (Fig. 248). Here some of the leaves, spreading out near the surface of the ground, have broad pinnæ and are

FIG. 248. The Hard Fern (*Blechnum spicant*), showing foliage-leaves and sporophylls. [Photo. E. J. S.]

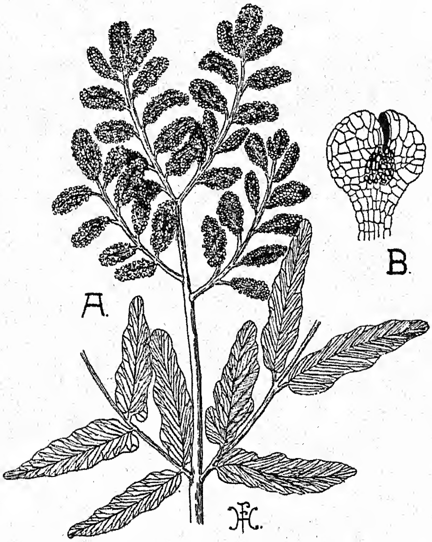


FIG. 249. A, Small part of a frond of the Royal Fern (*Osmunda regalis*), showing sterile pinnules (below) and fertile pinnules (above). (About half natural size.) (Original.) B, Single sporangium (after Luersen).

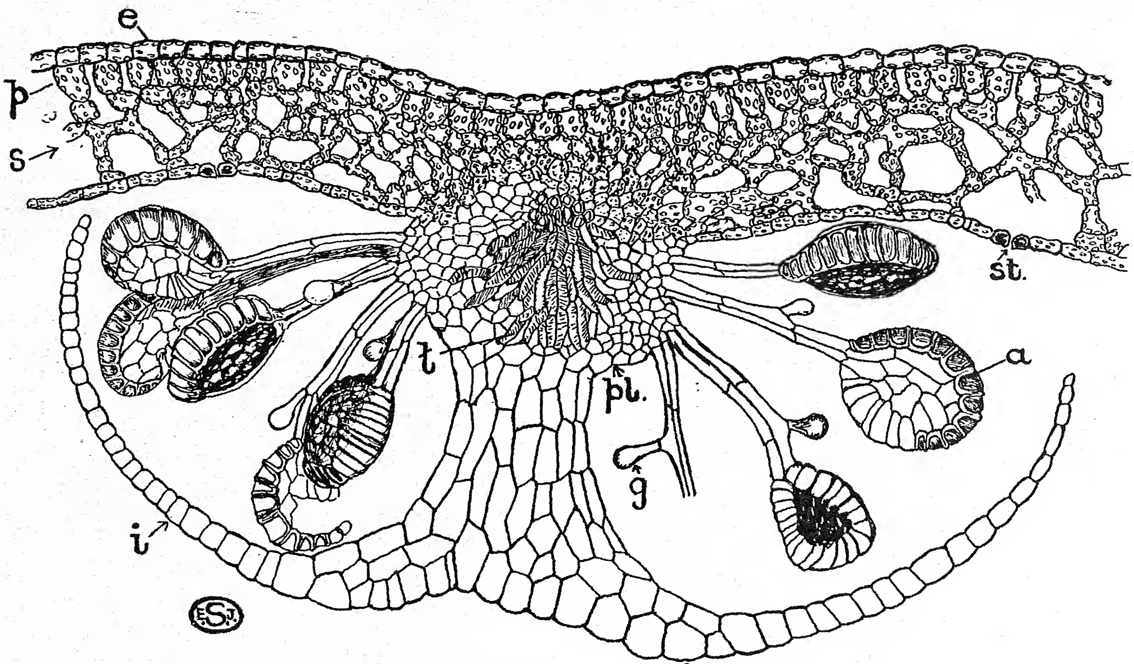


FIG. 250. Transverse section of a pinna, passing through a sorus, of the Male Fern (*Nephrodium filix-mas*), showing the indusium (*i.*), the placenta (*pl.*), and sporangia in various positions and stages of development. *a.*, annulus; *e.*, epidermis; *g.*, gland on sporangial stalk; *p.*, palisade tissue; *s.*, spongy tissue; *st.*, stoma; *t.*, tracheids.

purely vegetative, whilst others, which assume an erect position, have narrow lobes and are almost entirely concerned in the production of sporangia. Such fertile leaves are called *sporophylls*.

A less marked specialisation is seen in *Osmunda regalis*, where the lower part of the huge frond is sterile, whilst the upper pinnules, bearing the sporangia on both sides, exhibit practically no lamina (Fig. 249, A). In this connection it may be noted that in some tropical Ferns (e.g. *Platycerium*), which grow aloft on the branches of trees (a habit commonly seen in the Polypody in this country, Fig. 360), the lowest leaves are modified to form an oblique bracket by which humus is retained. A greater contrast between leaves and sporophylls is met with in other groups of Pteridophyta.

In transverse sections through a fertile pinnule of *Nephrodium filix-mas* (Fig. 250), the bulging placenta (*pl.*) on the under side is seen to be supplied by tracheids (*t.*) from the overlying vascular bundle. The indusium (*i.*) appears as an umbrella-shaped outgrowth, one layer of cells thick, arising from the top of the placenta. On the sides of the latter are borne numerous sporangia in various stages of development.

A mature *sporangium* (cf. also Fig. 251, B) consists of a stalk of usually three rows of elongated cells, terminated by a biconvex *capsule* which is more or less oval in side-view, and encloses the spores within a wall of a single layer of cells. The cells of the wall fit firmly together, and most of them are thin-walled and very flat, appearing more or less polygonal in surface-view, but tabular in optical section. The edge of the capsule, however, is occupied by a single row of specially differentiated cells. The greater part of this band, from the base of the capsule on one side to half-way down the other edge, is composed of cells which have all but their outer walls thickened, and which constitute the *annulus* (*a.* in Fig. 250 and *an.* in Fig. 251, B). The remainder, forming the so-called *stomium*, are much broader and thin-walled throughout (Fig. 251, B, *s.*), and it is here that the mature capsule ruptures.

Each sporangium arises as a papillate outgrowth from a single surface cell of the placenta, which is cut off by a cross-wall, and undergoes division by three oblique septa to produce a tetrahedral apical cell (Fig. 251, C, I, II). The three rows of segments, primarily cut off parallel to the three flat faces of the latter (III), elongate and become the stalk. Next, walls are formed parallel to all four faces of the apical cell (IV), and give rise to the one-layered capsule-wall (Fig. 251, D and E, *w.*), an inner nutritive layer, or *tapetum* (*t.*), and a central cell, the *archesporium* (*a.*). The last-named divides to form the *spore mother-cells*, each of which gives rise to four spores, the first of the two divisions in each

mother-cell being a reduction division. The development of the spores takes place at the expense of the food-materials contained in the granular thin-walled cells of the tapetum, which thus disorganises before the sporangium matures.

The four nuclei, produced in the spore mother-cell, usually become grouped so as to form a tetrahedral figure. Each, together

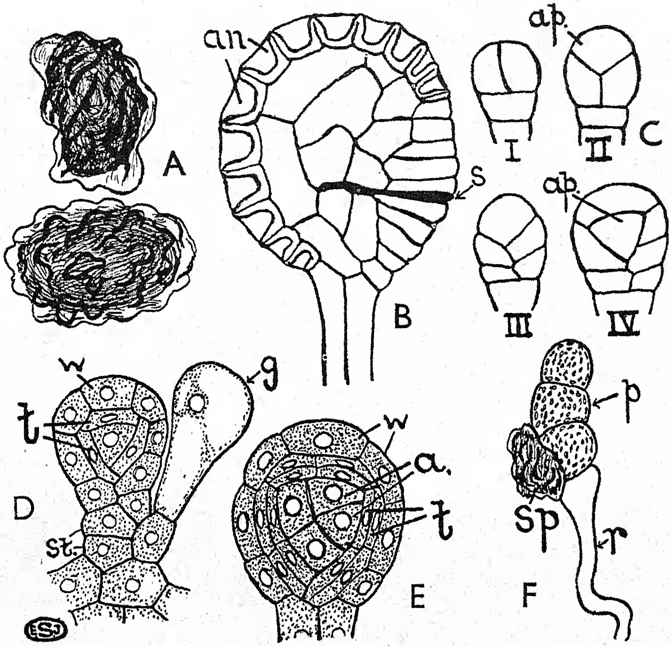


FIG. 251. *Nephrodium filix-mas.* A, Mature spores, greatly magnified. B, A single sporangium, showing the annulus (*an.*) and stomium (*s.*). C, Early stages (I–IV) in the development of the sporangium (after Müller). D and E, Successively later stages. *a.*, archesporium; *ap.*, apical cell; *g.*, gland; *St.*, cells of stalk; *t.*, tapetum; *w.*, wall. F, Germinating spore (*sp.*). *p.*, beginning of prothallus; *r.*, rhizoid.

with part of the cytoplasm, becomes surrounded by a separate wall, the whole of the contents of the mother-cell being thus used up to form four spores. Their faces of contact are more or less flattened and triangular, while the outer walls are convex, so that each spore, at its inception, has the form of a tetrahedron with a rounded base (cf. Fig. 263, D). Often, however, the spores round off after the mother-cell membrane has broken down.

With the ripening of the sorus the indusium dries and shrivels, exposing the sporangia, which likewise begin to lose moisture.

As evaporation proceeds, the thin outer walls of the annulus commence to bulge inwards (cf. Figs. 250 and 251, B), owing to the gradual reduction in the volume of their sap. The marked thickening of the walls, transverse to the annulus as a whole, resists lateral shrinkage and thus restricts contraction to the longitudinal direction. Hence an increasing tension is set up in the annulus, which eventually leads to rupture of the capsule-wall along the plane of greatest weakness, viz. the junction between the transversely extended cells of the stomium (Fig. 251, B). On the release of the tension, the annulus, carrying with it a great part of the capsule-wall and many of the contained spores, bends back until evaporation is sufficient to overcome the force of adhesion between the water in the cells of the annulus and the wall. When this separation takes place, the annulus flies back and the spores are shot out as from a sling; they are further dispersed by air-currents, and may thus be carried to a considerable distance. Rupture of the ripe sporangia can be observed under the microscope by adding glycerine.

The sporangia of the Bracken, and most other British Ferns, agree in all essential respects with those of the Male Fern. In the Royal Fern (*Osmunda regalis*), however, the sporangia are short-stalked and pear-shaped. Dehiscence takes place by a vertical split starting from a group of thick-walled cells, a little below the summit of the sporangium, and extending over the top of the latter and some way down the opposite face (Fig. 249, B).

The spores of most Ferns retain their capacity for germination for some time. In their thick walls three layers can often be distinguished, of which the outermost, usually dark-coloured and opaque (Fig. 251, A), is cuticularised, and constitutes the principal protective covering, whilst the innermost is thin and elastic. In germination (Fig. 251, F) the outer coats (*Sp.*) are burst, and the innermost is stretched to form a long, colourless, tubular outgrowth, which becomes separated off from the main body of the spore by a transverse wall, and penetrates the soil as the first *rhizoid* (*r.*) of the future plant. The remainder of the spore-contents, enveloped by the innermost layer of the wall, lengthen into a short horizontal filament (*p.*) whose few cells contain chloroplasts. Within the terminal cell two intersecting walls soon arise, and the apical cell thus formed cuts off segments on either side, so that the filament widens into a flat plate.

As the front margin broadens, two or more of its cells become meristematic (Fig. 252, *g.p.*) and development proceeds rapidly; at the same time horizontal divisions in the middle region of the plate form the *cushion*, which is several cells thick. The green thalloid plant thus established is known as a *prothallus*, and when

mature is usually heart-shaped, sometimes attaining a diameter of over a centimetre (Fig. 252). All the cells are alike and contain chloroplasts. From the under side, especially in the region of the cushion, scattered superficial cells grow out as colourless

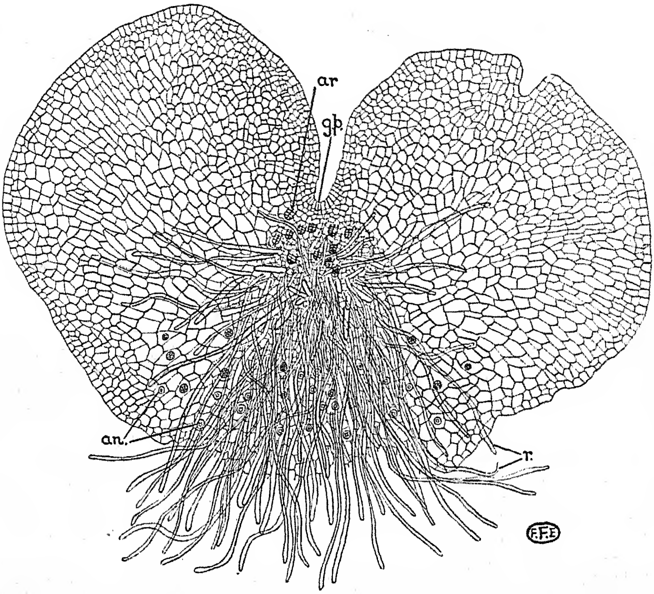


FIG. 252. Fern-prothallus, from the under surface (magnified about twenty times). A considerable number of antheridia (*an.*) are seen, on the older part, and the projecting necks of twelve archegonia (*ar.*), in the region of the cushion, from which also numerous rhizoids (*r.*) arise. *g.p.*, meristem.

rhizoids (*r.*), which serve for anchorage and the absorption of moisture.

When the prothalli grow densely crowded, they often remain more or less filamentous, a condition which is normal for most of the Filmy Ferns.

The prothallus is the Fern-plant (*gametophyte*) that bears the sexual organs. These are of the same general type as in Bryophyta, and are produced by the outgrowth of single cells, situated on the lower surface. Both kinds usually occur on the same prothallus (Fig. 252). The *antheridia* (*an.*), found mainly on the thinner marginal wings and the less robust prothalli, are almost spherical structures (Fig. 253, *g.*) with a small number of relatively large spermatozoid mother-cells (*s.*). The enveloping wall (*w.*) is peculiar in being composed only of two superposed ring-shaped cells surmounted by a dome-shaped cap-cell (Fig. 253, *e*). The

spermatozoids (Fig. 253, *d*), which are developed in the same way as in the Bryophyta (cf. p. 358), have a spirally coiled, spindle-shaped body bearing numerous flagella near the pointed end. Dehiscence of the antheridium, by the breaking away or rupture of the cap-cell (Fig. 253, *e* and *f*), takes place in wet weather, and

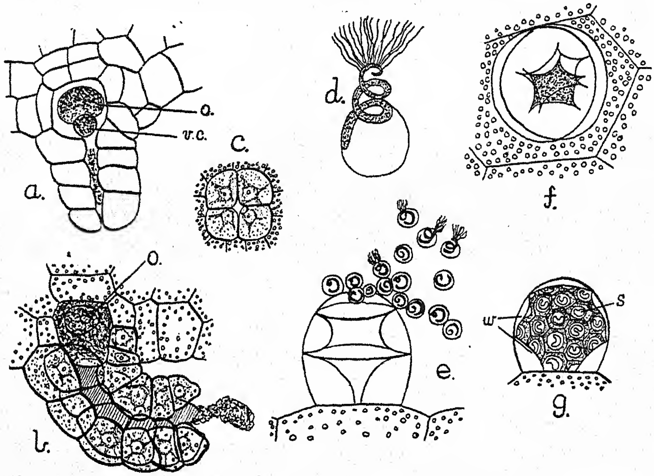


FIG. 253. *a–c*, Archegonia, *e–g*, Antheridia, and *d*, Single spermatozoid of the Fern. *a*, Immature, and *b*, mature, archegonium in longitudinal section; *c*, Neck in surface-view. *o.*, egg; *v.c.*, ventral canal cell. *g*, Almost mature antheridium in optical section, showing the wall (*w.*) and the spermatozoid mother-cells (*s.*); *e*, Dehiscing antheridium with the escaping spermatozoids; *f*, Dehisced antheridium from above. (*a*, after Goebel; the remainder after Kny.)

the liberated spermatozoids swim in the film of water retained by capillarity between the lower surface of the prothallus and the soil.

The *archegonia* are restricted to the region of the cushion, in which they are partially embedded, the necks alone projecting (Fig. 252, *ar.*; Fig. 253, *a* and *b*). The necks are all curved towards the pointed end of the prothallus, and differ from those of a Bryophyte archegonium in being short and composed of only four longitudinal rows of cells (Fig. 253, *c*), whilst there is but a single canal cell. The venter, containing the egg (*o.*) and the ventral canal cell (*v.c.*), appears as a mere cavity in the tissue of the prothallus. At maturity (Fig. 253, *b*) the four cells at the top of the neck are forced apart by a mucilage containing malic acid, formed during the disorganisation of the canal cells, and an open passage is thus left leading down to the egg. It is apparently the malic acid that attracts the spermatozoids to the archegonia.

After fertilisation the ovum becomes enveloped by a thin membrane, and divides by three successive walls into octants of a sphere (Fig. 254, A). Their further segmentation leads to the differentiation of four apical cells, which are situated one in each quadrant, and which respectively give rise to the root, the

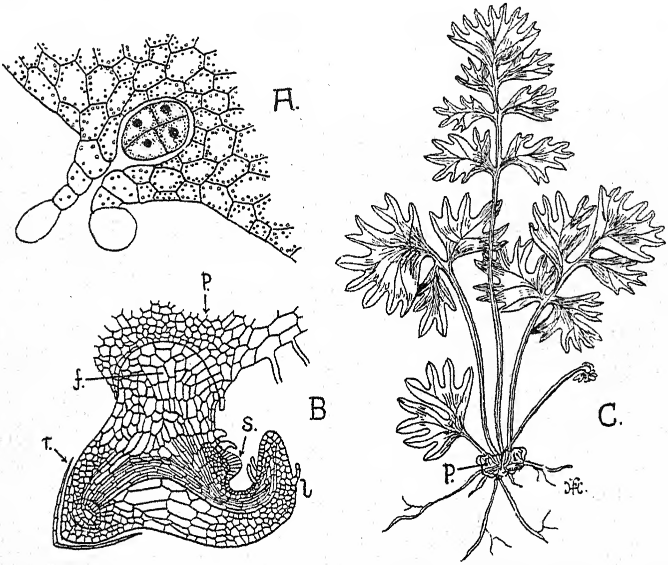


FIG. 254. Embryology of the Fern. A, Longitudinal section through an archegonium, showing the octant-stage in the division of the fertilised egg (after Sadebeck). B, Young embryo escaping from the prothallus (*p.*) (after Hofmeister). *f.*, foot; *l.*, first leaf; *r.*, first root; *s.*, stem. C, Young plant, with the remains of the prothallus (*p.*) at the base, four unfolded leaves of increasing complexity, and one leaf not yet unfolded (original).

stem, the first leaf, and the "foot" of the *embryo*. The *foot* develops as a large parenchymatous sucker which becomes firmly lodged in the tissue of the cushion, from whose cells it absorbs nourishment for the young Fern (Fig. 254, B, *f*).

By this means rapid growth of the root (Fig. 254, B, *r.*) takes place, and it soon pierces the prothallus and penetrates into the soil. Simultaneously the first leaf (*l.*), carrying with it the still rudimentary stem (*s.*), emerges on the lower side, and, arching up through the notch at the front end of the heart-shaped prothallus, exposes its green blade to the light. The stem now grows more vigorously, giving rise to adventitious roots which replace the short-lived primary root, and it is not long before further leaves

develop (Fig. 254, C). The latter, however, show but a very gradual increase in complexity, from the first, often almost undivided leaf, to the normal compound foliage of the adult Fern, which is frequently only attained after the lapse of several years. Production of sporangia is generally deferred till this stage is reached.

The young Fern, like the sporophyte of Liverworts and Mosses, is thus for a time dependent for nourishment on the prothallus.

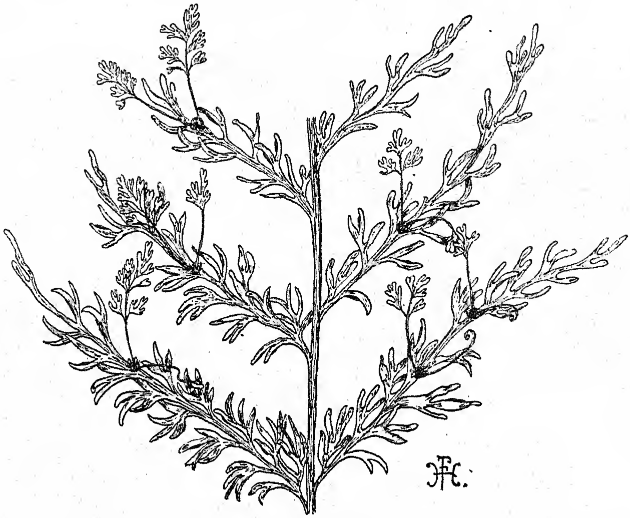


FIG. 255. Small part of a frond of *Asplenium bulbiferum*, showing the vegetative production of new plants (about half natural size).

But, as soon as the root has become established in the soil and the first leaf has spread out its lamina to the light, this dependence ceases and, soon after, the prothallus withers away (cf. Fig. 254, C). As compared with Bryophyta, the relative importance of the two phases in the life-history is therefore reversed. The free-living sporophyte usually attains large dimensions and exhibits a complexity of structure which is only approached by the perennial gametophytes of some few Mosses. On the other hand, the sexual generation is as a general rule short-lived, though in a few Ferns (e.g. *Osmunda*) it persists for some years. Normally the two generations alternate regularly with one another, but occasional abnormalities are encountered.

Thus, in certain Ferns the prothalli may arise by direct budding from the leaves or sporangia, without the formation of spores (*apospory*), a condition that has been experimentally induced in a variety of the Lady Fern by pinning detached segments of the

fronds on damp sand. Sometimes the sporophyte develops vegetatively from the prothallus without the intervention of sexual organs (*apogamy*). Vegetative multiplication of the sporophyte is not infrequent, new plants arising from buds formed on the surface of the fronds, as in the commonly cultivated *Asplenium bulbiferum* (Fig. 255).

In the normal life-cycle, of Bryophyta and Pteridophyta alike, the spore is the starting-point of the sexual, and the fertilised egg of the asexual, generation. The spore mother-cells, with few exceptions, give rise to four spores, after undergoing two successive nuclear divisions. The first of these involves the passage of entire chromosomes to the two poles of the dividing nucleus, as a result of which their number is halved. The two successive divisions produce four haploid spores. The diploid number is restored by sexual fusion. The sexual generation is thus haploid and the asexual diploid. The alternation in Ferns and other Pteridophyta is similar to that exhibited by *Laminaria* (p. 314).

[For further details on Ferns, see F. O. Bower, *Primitive Land Plants*, Macmillan & Co., 1935 (658 pp.), a good brief account; a much more extensive treatment by the same author is: *The Ferns*, 3 vols., Cambridge Botan. Handbooks, Cambridge Univ. Press, 1923–28. For taxonomic works, see p. 578.]

CHAPTER XXXII

HORSETAILS (EQUISETALES) AND CLUBMOSSES (LYCOPODIALES)

THE Ferns (*Filicales*) alone of the existing groups of Pteridophyta are widely represented at the present day. Not only are they almost ubiquitous in their distribution, but they comprise a large number of families and genera. The Bracken in North Temperate zones, and *Gleichenia* in the Tropics, illustrate, moreover, the important rôle played by Ferns in many types of vegetation.

The Horsetails (*Equisetales*) and Clubmosses (*Lycopodiales*),[1] on the other hand, which, like the Ferns, have been traced back in the fossil state to very early periods of the earth's history, are now only represented by a few very distinct genera. These groups flourished vigorously, however, at the period when the Coal Measures were laid down; then they comprised woody plants which, in great part, attained to the dimensions of trees (Fig. 259). These features have been lost by the living forms of the present day, which are mostly small perennials. It is, indeed, probably correct to regard the remote past as the age of trees and the present rather as that of herbs.

By contrast with Ferns the leaves of Horsetails and Clubmosses are remarkably small and simple in form, so that the habit of the plant is here determined mainly by the character and extent of branching of the stem (Fig. 256, A and C; Fig. 262, A). The Horsetails (*Equisetum*) are switch-plants (Fig. 256, A and C and p. 504) whose green, longitudinally furrowed stems bear whorls of brownish scale-leaves fused to form a toothed sheath (*s.l.*) around each node. The branches are likewise whorled (Fig. 256, C), and, since they arise relatively late, have to pierce their way through

[1] For a more extensive treatment, see F. O. Bower, *Primitive Land Plants*, Macmillan & Co., 1935 (658 pp.). For fossil Pteridophyta consult D. H. Scott, *Studies in Fossil Botany*, 2 vols., A. & C. Black, 3rd. edit., 1923, a general anatomical and morphological account; and A. C. Seward, *Fossil Plants*, 4 vols., Cambridge Univ. Press, 1898–1919, a comprehensive taxonomic account of fossil plants.

the bases of the fused leaves. The erect shoots are the upturned ends of the branches of underground rhizomes (Fig. 256, A), which bear similar whorls of scale-leaves, as well as numerous adventitious roots, at each node. The rhizome of the Field Horsetail (*Equisetum*

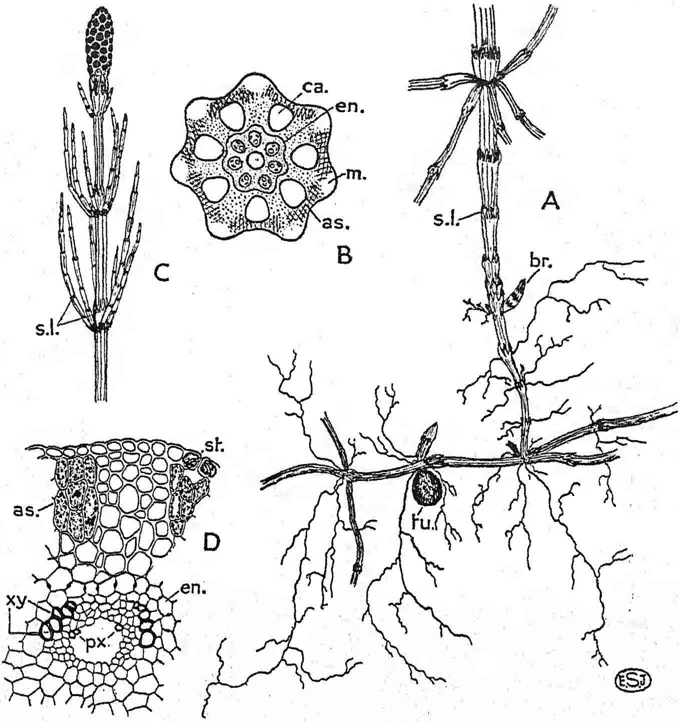


FIG. 256. *Equisetum.* A, Lower part of aerial shoot of *E. arvense*, attached to the rhizome; *br.*, branch; *s.l.*, scale-leaves forming whorl at node; *tu.*, tuber. B, Diagram of transverse section of stem of same; *as.*, photosynthetic tissue; *ca.*, air-canal in cortex; *en.*, endodermis surrounding the seven vascular bundles; *m.*, mechanical tissue. C, *E. palustre*, upright fertile shoot with terminal cone. D, Portion of a transverse section of a stem of same showing the photosynthetic tissue (*as.*), the endodermis (*en.*), a stoma (*st.*), the protoxylem-canal with protoxylem elements (*px.*) at its margin and the metaxylem (*xy.*).

arvense) bears easily detached tubers (Fig. 256, A, *tu.*) which are formed from modified branches and are a prolific means of vegetative reproduction. In the ancient Horsetails (*Calamites*) of the Palæozoic, the leaves were larger (cf. Fig. 257, B) and, like the branches, were whorled.

The *anatomy* of the stem (Fig. 256, B, D) superficially resembles

that of a Dicotyledon in the arrangement of the vascular tissues and shows groups of photosynthetic tissue (*as.*) opposite the shallow furrows in which the stomata are situated. It invariably shows great reduction of the xylem and a conspicuous system of air-canals in the cortex and pith (Fig. 256, B, D). These aquatic characteristics (cf. p. 544) are to be expected in partially submerged

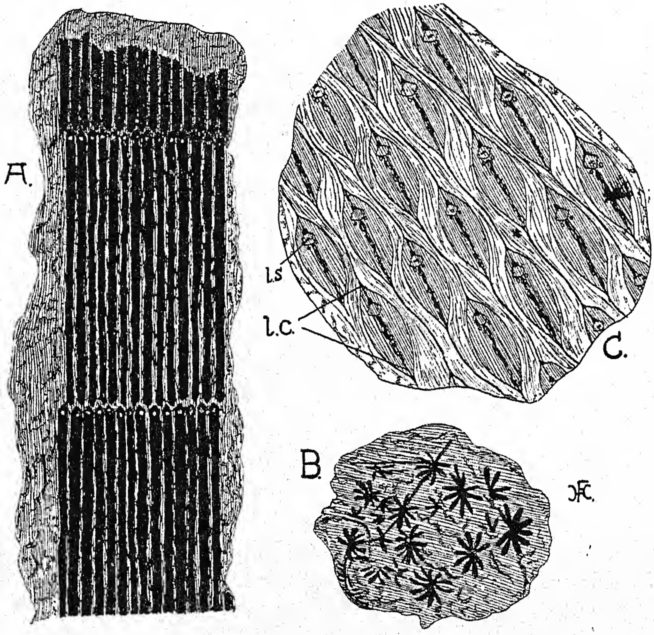


FIG. 257. Common forms of preservation of the fossil Horsetails and Club-mosses. A, Pith-cast of *Calamites*. B, *Annularia sphenophylloides*, the foliage of *Calamites*. C, Small part of the surface of the stem of a *Lepidodendron*, showing the characteristic leaf-cushions (*l.c.*); *l.s.*, leaf-scar.

species like *Equisetum limosum* and *E. palustre*, but the fact that others (e.g. *E. arvense*), growing in relatively dry situations, nevertheless exhibit these features may indicate that the genus as a whole is derived from aquatic ancestors. Indeed, there is good evidence that the *Calamites* of the Coal Measures, which exhibited similar features combined with pronounced secondary thickening, were inhabitants of swamps.

The sporangia of Horsetails are borne on little mushroom-shaped *sporophylls* (Fig. 258, B), differing widely from the ordinary leaves, and collected together at the ends of the stems to form *cones* or *strobili* (Fig. 256, C; Fig. 258, A). These usually

terminate the ordinary vegetative shoots, though in the Field Horsetail (*E. arvense*) they are found in spring on special shoots distinguished by their brown colour and the absence of branches. Each peltate sporophyll is perpendicular to the main axis, and bears on the inner face of its hexagonal lamina a ring of 5 to 10 sporangia encircling the stalk (Fig. 258, B). In the young cone the heads of the sporophylls fit closely together, thus forming a compact protection for the sporangia; but as the latter mature the sporophylls separate, through elongation of the axis, and permit escape of the green spores. The individual sporangia are rather larger than those of Ferns, and have a several-layered wall. Many of the fossil Horsetails possessed cones of more elaborate structure.

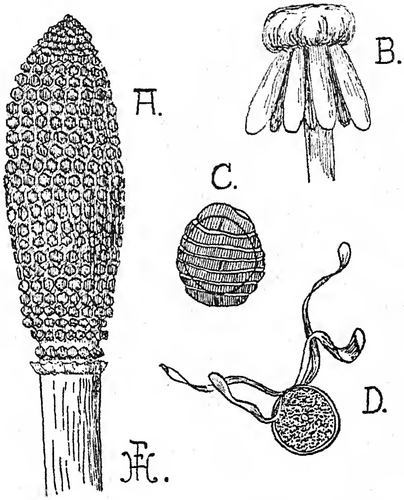


FIG. 258. A, Entire cone, and B, Single sporophyll of *Equisetum maximum* (original). C and D, Mature spores, showing the splitting of the outer coat. (C, after Sachs; D, after Dodel-Port).

At maturity the outermost coat of each spore consists of four extremely hygroscopic spiral strips (Fig. 258, C, D) which only remain attached at one point. Groups of spores consequently tend to be entangled when the contents of a sporangium are scattered by the wind, and this may be of importance, since the archegonia and antheridia are usually produced on distinct *prothalli*. The spores are, however, all alike, the sex of the resulting prothalli depending on the conditions of nutrition, those poorly nourished becoming male, whilst those well nourished become female. Both kinds are more or less richly branched, but the male are much smaller than the female. The sexual organs borne upon them do not differ markedly from those of Ferns. It may be noted that, when Fern prothalli grow densely crowded, they often bear antheridia only, although unisexuality is here the exception rather than the rule.

The present-day Clubmosses are represented mainly by the genera *Lycopodium* (Fig. 261, A) and *Selaginella* (Fig. 262). The Quillwort (*Isoëtes lacustris*, Fig. 260), which occurs submerged in

mountain tarns, is a peculiar member of this group, many of whose features recall those of the fossil Clubmosses (*Lepidodendron*, Fig. 259). Fragments of the stems of *Lepidodendron* with, or often without, the leaves are very common in the Coal Measures and are readily identified by their characteristic markings (Fig. 257, C).

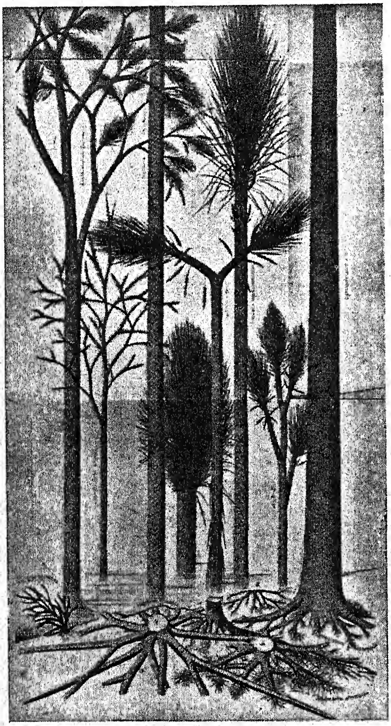


FIG. 259. Restoration of various fossil Clubmosses (*Lepidodendron* and *Sigillaria*). (After Grand Eury.)

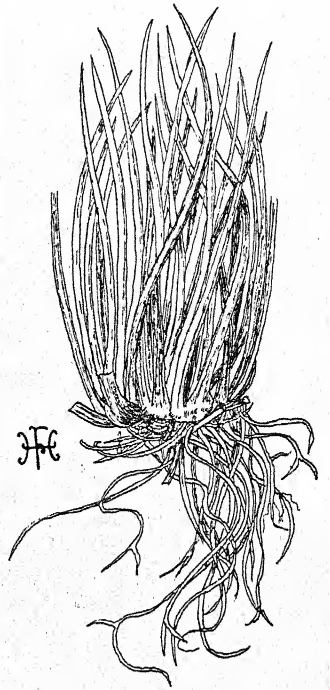


FIG. 260. The Quillwort (*Isoëtes lacustris*), somewhat reduced.

The small spirally arranged leaves of *Lycopodium* densely clothe the stems, which are either erect, as in the Fir Clubmoss (*L. selago*), or prostrate, except for the cone-bearing shoots, as in *L. clavatum* (Fig. 261, A). The stems, as well as the occasional adventitious roots, exhibit forked branching, and never contain more than a single rather root-like stele,[1] whose detailed structure is often somewhat complex. The sessile leaves are attached by a broad cushion-

[1] A single stele was likewise found in *Lepidodendron* where, however, it became enveloped by a broad zone of secondary wood and phloem.

like base, and are traversed by but a single median vein (Fig. 261, B); the same obtained in *Lepidodendron*, the persistent leaf-cushions (Fig. 257, C, *l.c.*) affording the distinctive markings above referred to. The British species of *Lycopodium* are found in moist upland pasture, except for *L. inundatum*, which occurs in lowland bogs.

The *sporophylls* (Fig. 261, B) are similar to the foliage-leaves,

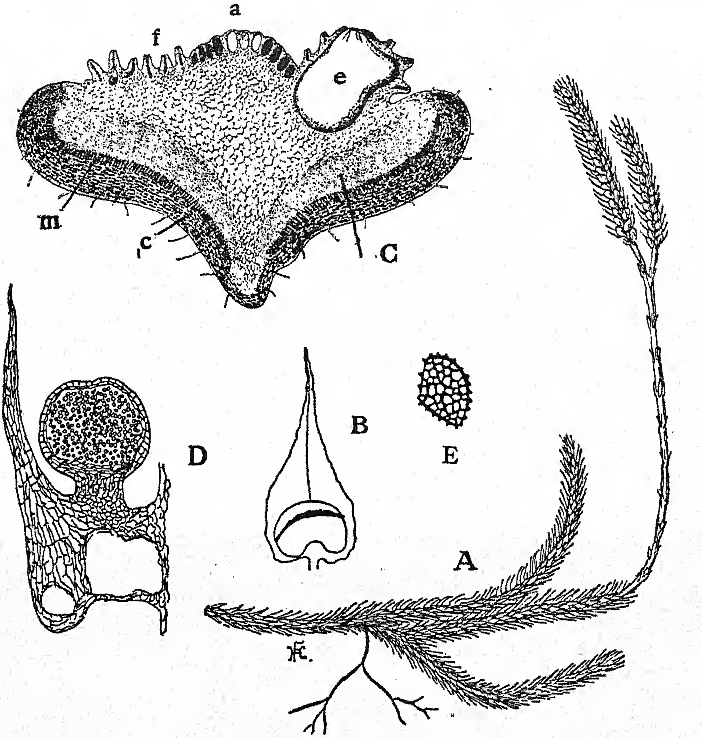


FIG. 261. *Lycopodium*. A, Small part of a plant of *L. clavatum*, with a fertile shoot bearing two cones. B, Single sporophyll of same, with a dehiscent sporangium. C, Prothallus of *L. clavatum* in longitudinal section, showing antheridia (*a*), archegonia (*f*), and a developing embryo (*e*). *c.*, cortex; *m.*, mycorrhizal layer. D, Longitudinal section of sporophyll with sporangium. E, Spore. (B, after Strasburger; C, after Bruchman; the rest original.)

and are commonly in whorls; they are readily recognised by the single large, somewhat kidney-shaped, sporangium which each bears on its upper surface. In most species the sporophylls are aggregated in cones, as in *Equisetum*, although in *L. selago*, for example, the reproductive region is not clearly marked, zones of sporophylls usually alternating with vegetative leaves. Another

peculiarity of this species is the development of large *bulbils* in the axils of the uppermost leaves; these structures, which serve for vegetative reproduction, must not be mistaken for sporophylls.

The *cones*, when present, occupy the ends of erect branches, which are of the ordinary type, except in *L. clavatum* (Fig. 261, A); here they bear minute leaves, at rather wide intervals, contrasting

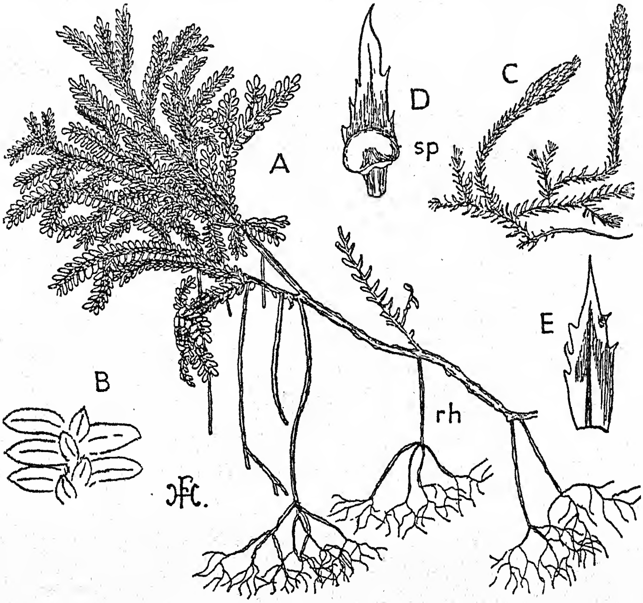


FIG. 262. A and B, *Selaginella martensii* (original). A, Part of a plant showing the leafy shoots, the rhizophores (*rh.*), and the roots arising from their ends. B, Small part of a branch enlarged, to show the two kinds of leaves. C, Plant of *S. spinosa* (after Wettstein), showing two cones. D, Sporophyll, and E, foliage-leaf of *S. spinosa* (after Hieronymus). *sp.*, sporangium.

markedly with the densely arranged sporophylls of the cone. Each sporangium contains numerous spores (Fig. 261, D) which, after being shed, give rise to peculiar fleshy *prothalli* (Fig. 261, C). In most species these grow underground as saprophytes, obtaining their food with the aid of a mycorrhiza (*m.*) from the humus in which they are embedded, but despite this fact they show rather more anatomical differentiation than is usual in prothalli. Some species exhibit a slight development of green leafy lobes at the surface. Archegonia (*f*) and antheridia (*a*) are borne on the same prothallus (Fig. 261, C).

Although *Selaginella* is represented in Britain only by *S. spinosa* (Fig. 262, C), which is found in similar habitats to those frequented

by our species of *Lycopodium*, several members of the genus are commonly cultivated. The general habit is like that of *Lycopodium*, but in most species the leaves are arranged in four rows, two comprised of small leaves situated on the upper side of the stem, and two of large leaves towards the lower side (Fig. 262, A and B); at each node there is one large and one small leaf. The British *S. spinosa*, in which the habit is erect, possesses leaves that are all alike (Fig. 262, C).

In many *Selaginellas* the method of rooting is peculiar, the roots arising from special leafless branches known as *rhizophores* (Fig. 262, A, *rh.*). These are formed in pairs at the points of forking of the stems, but usually only one member of each pair develops. This grows downwards, generally forking repeatedly, and, on reaching the soil, roots originate from the swollen tips of the ultimate branches.

The stem is traversed by one or few steles,[1] essentially like those of Ferns, except that each is surrounded by an air-space, which is bridged either by strands of cortical cells, or by radially elongated endodermal cells. The roots and rhizophores are peculiar in exhibiting but a single protoxylem group.

The *cones*, again situated at the ends of usually erect branches (Fig. 262, C), exhibit four rows of sporophylls, all of the same size and shape, and each with an axillary sporangium borne on a short stalk (Fig. 262, D, *sp.*; Fig. 263, A, E). The sporangia are of two kinds: the one kind (microsporangia), generally found towards the apex of the cone, are filled with numerous small *microspores* (Fig. 263, A, *mi.*); the other kind (megasporangia) each contain only four large *megaspores* (Fig. 263, A, *mg.*). These features are readily observed in longitudinal sections through the cones, which also show the presence of a small outgrowth (the *ligule*, Fig. 263, *l.*) from the upper surface of each sporophyll, between its upturned tip and the sporangium. Such ligules, though most conspicuous on the sporophylls, occur also on all the vegetative leaves, but their function is obscure. A ligule is not met with in the genus *Lycopodium*, but occurs in *Isoëtes* and appears to have been characteristic of most of the extinct representatives of the family, which also possessed two kinds of spores.

The young sporangia of *Selaginella* have a several-layered wall, enclosing a large number of spore mother-cells, and, up to this stage, all are alike. In the microsporangia each mother-cell gives rise to four small spores, but in the megasporangia only one develops further, enlarging rapidly at the expense of the others, and dividing to form the single tetrad (Fig. 263, A). An American species

[1] One in *S. spinosa*, three in *S. kraussiana*.

(*S. rupestris*) exhibits an even greater reduction, since occasionally only one of the four megaspores reaches maturity, and, in this and certain other species, the spores are retained within the sporangium until after the fertilisation of the archegonia produced in the resulting prothalli. Both kinds of sporangia dehisce by a wide slit, the spores ordinarily maturing their prothalli on the ground.

The contents of the microspore divide to form a few-celled,

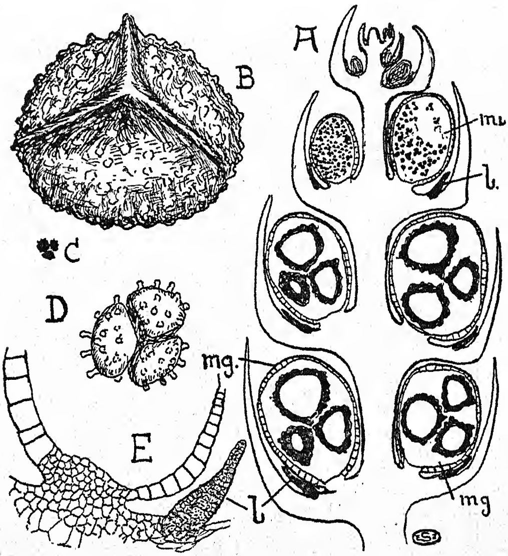


FIG. 263. *Selaginella umbrosa.* A, Longitudinal section through part of a cone, showing microsporangia (*mi.*) above and megasporangia (*mg.*) below. E, Small part of megasporangium enlarged to show the stalk and wall. *l.*, ligule. B, Single megaspore enlarged. C, Tetrad of microspores on the same scale of magnification as B. D, Tetrad of microspores enlarged.

exceedingly reduced *male prothallus*, developing neither chloroplasts nor rhizoids, and consisting in the main of a small number of spermatozoid mother-cells (Fig. 264, *f*). The resulting biflagellate spermatozoids (Fig. 264, *d*) are liberated, during wet weather, by the rupture of the coats of the microspores.

The *female prothallus* begins to develop within the megaspore long before the latter is shed, and, like the male, exhibits considerable reduction and usually remains colourless. The early stages of its formation are characterised by repeated division of the megaspore-nucleus, separating walls only arising much later. When ready for fertilisation the prothallus consists of a small-celled

tissue, situated opposite the apex of the tetrahedral spore and exposed by the rupture of its coats (Fig. 264, *a* and *b*, *p*.), while the bulk of the spore-contents, still enclosed in the megaspore-wall, are occupied by large cells laden with food-material (*f*.). The few

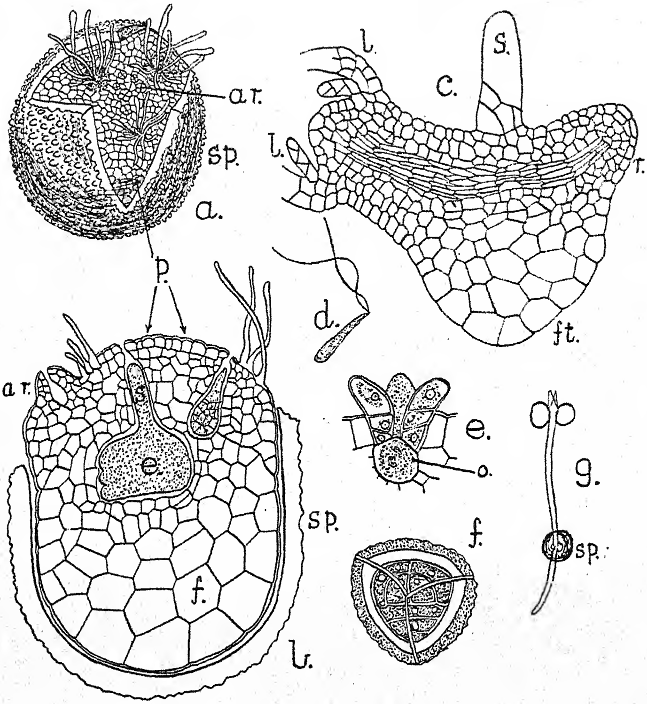


FIG. 264. *Selaginella*, prothallia and embryology. *a*, Front view, and *b*, Vertical section of mature megaspore with female prothallus; *c*, Older embryo; *d*, Spermatozoid; *e*, Archegonium in longitudinal section; *f*, Microspore with contained male prothallus; *g*, Young plant still attached to the megaspore (*sp*.). *ar*., archegonia; *e*., embryo (in *b*); *f*., large-celled nutritive tissue (in *b*); *ft*., foot (in *c*); *l*., leaves of embryo; *o*., egg (in *e*); *p*, prothallus; *r*., radicle; *S*., suspensor; *Sp*., coat of megaspore. (*a*, *e* and *g*, after Bruchman; *d*, after Belajeff; remainder after Pfeffer.)

archegonia, which have very short, scarcely projecting necks (Fig. 264, *e*), are embedded in the small-celled apical region (Fig. 264, *a*,*b*, *ar*.).

The fertilised egg divides transversely, the inner (lower) half giving rise to the *embryo* proper. The outer (upper) half, forming the so-called *suspensor* (Fig. 264, *b* and *c*, *S*.), divides a few times and elongates considerably, so that the developing embryo is

pushed down into the large-celled nutritive tissue (*f.*) below. The suspensor is a structure characteristic of the higher seed-plants, but in other essential respects the embryology resembles that of Ferns. Absorption of the stored food takes place by means of a sucker or foot (Fig. 264, *c*, *ft.*), but the young plant acquires independence at an early stage (Fig. 264, *g*).

Regarded as a whole, the Pteridophyta exhibit a great variety of vegetative structure, and considerable specialisation in their reproductive processes. They offer a marked contrast to the Bryophyta in the relative importance of the spore-producing phase, which is an independent plant highly adapted to a terrestrial existence. Associated with the last-named feature we see the differentiation of specialised conducting tissue and of true roots. There is, moreover, a marked tendency towards division of labour, on the one hand between vegetative and reproductive leaves, on the other between the prothalli. In the Ferns all the latter are alike and bear both kinds of sexual organs, although there are occasional exceptions when the conditions of nutrition are abnormal (cf. p. 389). This tendency leads to the development of definite unisexual prothalli in the Horsetails, which, however, like the Ferns, have only one kind of spore, *i.e.* are *homosporous*. *Lycopodium* resembles the Ferns in these respects, but in *Selaginella* and *Isoëtes*, not only are the prothalli unisexual, but they are produced from two kinds of spores, *i.e.* this genus is *heterosporous*.

Heterospory involves the risk of the two sexes of prothalli not germinating in sufficiently close proximity to one another. Certain advantages similar to those obtained by oogamy (cf. p. 309), obviously accrue, *e.g.* the provision by the mother-plant of an abundant store of food for the development of the new sporophyte. These reserves are laid down in the megaspore before it is shed, and, as a consequence, the resulting prothallus can dispense with rhizoids and a photosynthetic mechanism. Moreover, the embryo acquires additional protection during the early stages of its development from the coats of the megaspore, within which the greater part of the prothallus remains enclosed (cf. Fig. 264, *b.*). A further step would obviously be the retention of the megaspore within the sporangium until after fertilisation and during the development of the embryo, and this is the rule in the Spermaphyta. The microspores, requiring no appreciable amount of food-reserves, and being consequently of small dimensions, can be produced in large numbers. This affords an increased power of dispersal whereby the association of the two prothalli is rendered more probable.

CHAPTER XXXIII

CYCADS AND EXTINCT SEED-BEARING PLANTS

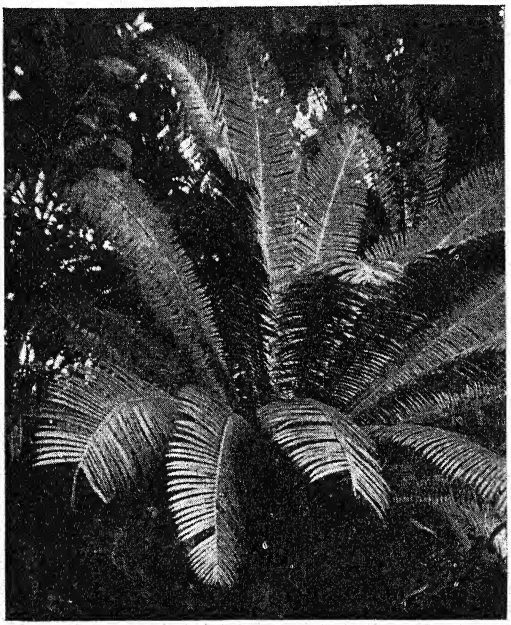
A GROUP may now be considered which, although portraying many of the characteristics of Flowering Plants, nevertheless shows several features reminiscent of Ferns. These are the *Cycads*,[1] which have a wide distribution in the tropical regions of America, South Africa, Eastern Asia, and Australia, though most of the genera have a very restricted range (cf. Fig. 416). Fossil records show the group to be a very ancient one that played a particularly important part during the Mesozoic period, the present-day representatives appearing merely as relics. The Sago-palm (*Cycas revoluta*) is in most respects typical of the living forms.

Most Cycads (Fig. 265) have the appearance of Palms or Tree Ferns, the often huge pinnate leaves forming a crown at the top of the partly subterranean and tuberous, or overground and columnar, stems which may attain a height of sixty feet. The trunk is rarely branched, and, in the older portion, its entire surface is covered with an armour formed by the large persistent bases of the leaves of previous seasons. Fresh leaves are produced at intervals, the outer ones of each crop being modified to form protective bud-scales. In some of the genera the unfolding leaves exhibit a spiral inrolling of the pinnæ (e.g. *Cycas*, Fig. 266), or of the midrib, similar to that characteristic of Ferns. Other resemblances to this group are to be found in the forked veining of the blades (Fig. 267, E) and in the structure of the petiole. The numerous vascular strands of the latter have the protoxylem embedded within the metaxylem, a feature especially characteristic of Ferns (cf. p. 372 and Fig. 243, *P.xy.*), whereas in the vast majority of the Seed plants the protoxylem of the stem is immediately adjacent to the pith (cf. p. 136).

Cycads often attain a great age and their stems exhibit secondary thickening like that of woody Dicotyledons. The pith is very large, and, in the Sago-palm, contains the stores of starch which are one of the sources of the sago of commerce.

[1] For reference-books, see p. 425.

The *sporophylls* are of two kinds, microsporophylls and megasporophylls, and are arranged in distinct male and female cones, borne on separate individuals. The *microsporophylls* are thick



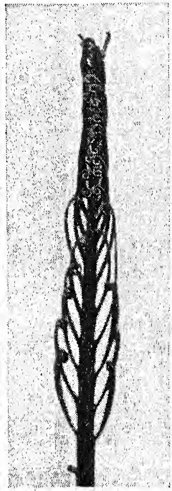


FIG. 265. Young plant of *Cycas circinalis*. [Photo. E. J. S.]
FIG. 266. Young leaf of *Cycas*, showing spiral inrolling of the pinnæ. [Photo. E. J. S.]

scales which are spirally arranged (Fig. 267, A), and bear, on their under-surface, numerous sporangia (Fig. 267, D), often collected together in small groups; they dehisce by a wide split. The *megasporophylls* are usually of a similar nature, although they produce only two megasporangia, often placed one on either side of the stalk-like lower part (Fig. 268, B); the megasporangia are of a peculiar type and are known as *ovules*. In *Cycas*, however, the megasporophylls resemble the foliage-leaves, although relatively small, hairy, and brown in colour, and often bear more than two ovules (Fig. 268, A). The female plant of *Cycas* can be compared with such a Fern as *Blechnum* (cf. p. 375), since in both the sporangia occur on fronds which are but little modified. An examination of the megasporophylls of different Cycads shows all stages in the reduction of the lamina to a condition in which the

leaf-like character is almost entirely obscured (e.g. *Encephalartos*, Fig. 268, B).

The *ovules* (*megasporangia*) (Fig. 268, C and D) are of considerable size, but contain only a single large megaspore (*p.*) within the several-layered parenchymatous wall or *nucellus* (*n.*). The delicate texture of the latter can be related to the presence of a thick protective covering (*o.* and *i.*). This integument completely envelops the nucellus, and is indeed fused with it except at its

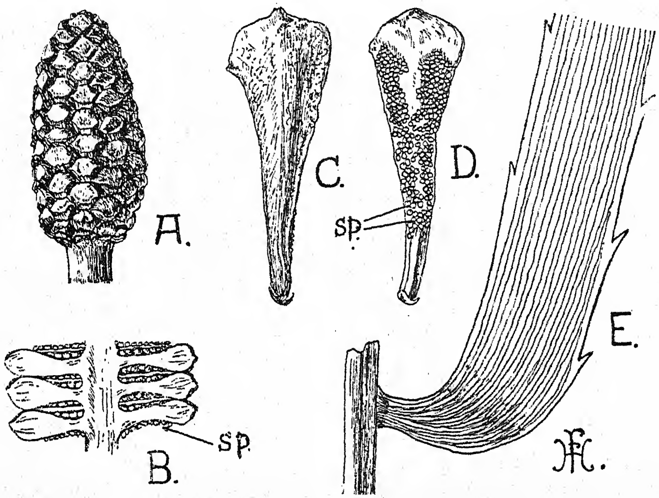


FIG. 267. A, Entire male cone of *Bowenia spectabilis*, and B, Part of the same in longitudinal section, showing the microsporangia (*sp.*) on the lower surfaces of the sporophylls. C, Upper, and D, Lower surface of a microsporophyll of *Cycas*. *sp.*, microsporangia. E, Part of a pinna of the leaf of *Encephalartos* to show the veining.

extreme apex. In this region the integument is pierced by a narrow canal, the *micropyle* (*mi.*), leading down to the *pollen chamber* (*p.c.*), which is a conical cavity formed by the breaking down of cells in the tip of the nucellus. The ovule is supplied by two vascular strands from the sporophyll. These fork at its base to form two systems of branches, extending almost to the extreme tip: those of the outer series (*o.b.*) traverse the peripheral layers of the integument, whilst those of the inner (*i.b.*) run close to the line of junction of the latter and the nucellus.

The wind- or insect-borne microspores (*pollen grains*) are drawn into the pollen chamber by the drying up and contraction of the mucilaginous fluid (formed by the disintegrating cells of the nucellus) which exudes from the micropyle at the time of

pollination. Within the pollen chamber germination ensues (Fig. 268, C, and 269, C), and a short branching sucker-like pollen tube (*p.t.*) grows into the adjacent tissue of the nucellus.[1] Subsequently two *spermatozoids*, each with a spiral band of flagella [2] (Fig. 269, B, *s.*), are developed within the main body of the micro-

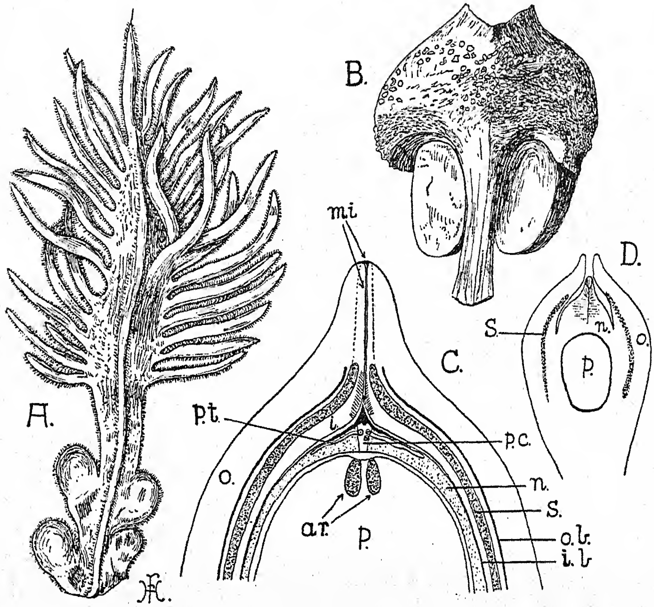


FIG. 268. A, Megasporophyll of *Cycas revoluta* with four ovules (about half natural size). B, Mature megasporophyll of *Encephalartos hildenbrandtii*, bearing two seeds (about half natural size). D, Diagram of longitudinal section of ovule of *Bowenia spectabilis*, and C, Front end of same enlarged. *ar.*, archegonia; *i.*, inner fleshy layer of integument; *i.b.*, vascular bundle of inner series; *mi.*, micropyle; *n.*, nucellus; *o.*, outer fleshy layer of integument; *o.b.*, bundle of outer series; *p.*, female prothallus within megaspore; *p.c.*, pollen chamber; *p.t.*, pollen tube; *s.*, stony layer of integument. (A and B, original; C and D, after Kershaw.)

spore. In the meantime the large megaspore has become filled with a uniform tissue, the *female prothallus* (Figs. 268, C, and 269, C, *p.*) which produces a, commonly small, number of archegonia (*ar.*), with very minute necks (*n.*) and large eggs (*o.*), at the end adjacent to the micropyle.

The nucellar tissue between the pollen chamber and the female

[1] The sequence of events in the germination of the microspores of Cycads is very similar to that in Conifers (cf. p. 421).

[2] Apart from the Cycads, the Maiden-hair Tree (*Ginkgo biloba*) is the only seed-plant which has flagellate, free-swimming sperms.

prothallus breaks down (Fig. 269, C), with the formation of a slimy fluid in which the liberated spermatozoids (*s.*) swim to the archegonia (*o.*), and in this way fertilisation is accomplished. The nucleus of the fertilised egg divides repeatedly to form numerous nuclei which, at least in the lower part of the oospore, become separated by cell-walls. It is this region alone that gives rise to

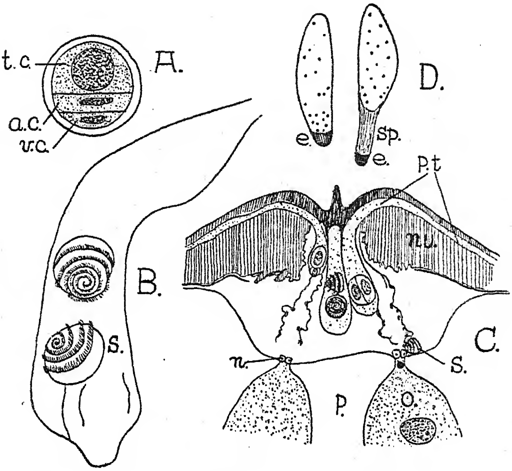


FIG. 269. A, Germinating microscope of *Cycas*, showing vegetative cell (*v.c.*), antheridial cell (*a.c.*), and tube cell (*t.c.*). B, Pollen tube with the two spermatozoids (*s.*). C, Diagram of longitudinal section through apex of nucellus (*nu.*) and female prothallus (*p.*) of *Dioon edule*, showing pollen tubes (*p.t.*) and pollen grains in various stages of development, spermatozoids (*s.*), and archegonia with eggs (*o.*) and necks (*n.*). D, Two proembryos of *Dioon edule*, the left-hand one younger than the right-hand one; the dotted part is the fertilised ovum. *e.*, embryo; *Sp.*, suspensor. (A and B, after Ikeno; C and D, from Chamberlain.)

the embryo (Fig. 269, D, *e.*), whilst the remainder serves for nutrition.

In each ovule only one *embryo* ultimately develops, its growth taking place at the expense of the surrounding prothallus, into the centre of which it is carried by the marked elongation of a suspensor (Fig. 269, D, *sp.*). Upon reaching a certain stage, however, in which two cotyledons, plumule, and radicle can be distinguished, the embryo becomes dormant, the residue of the female prothallus around forming a nutritive tissue, the *endosperm*. The whole is enveloped by the thick integument, now differentiated into three layers, which can even be recognised in an immature form in the young ovule. These layers comprise an inner (Fig. 268, C, *i.*), and a much thicker outer (*o.*), flesh, with an intervening very hard

stony layer (*s.*). This product of megasporangium, female prothallus, and embryo is a plum-like *seed*, many times the size of the original ovule.

The Cycads obviously show many superficial resemblances to Ferns, but these are even more pronounced in another group of plants (*Pteridosperms*) which, like the *Calamites* and *Lepidodendrons* of the Coal Measures, are known only as fossils. The members of this group, though closely resembling the Ferns in habit, show analogies with Cycads in their anatomy, their mode of reproduction, and especially in the possession of seeds.

A complete knowledge of such fossil plants [1] is only acquired gradually and as a result of prolonged research. At first the separate fragments of stem, root, leaves, etc., are studied as unrelated structures, but subsequently patient toil pieces them together till a more or less complete picture of the whole is obtained. The external appearance of a fossil plant is best appreciated from casts or impressions preserved in consolidated mud, sand, etc. Not infrequently, however, the tissues have been impregnated with silica, calcium carbonate, etc., so that the internal structure is recognisable. From such petrified portions thin slices, comparable to those prepared from a living plant, can be obtained.

Lyginopteris oldhamia, one of the commonest of the Coal Measure fossils, has been pieced together until it is known with a degree of completeness only shared by a few living plants. *Lyginopteris* was probably a woody scrambler, with relatively slender stems and large compound Fern-like leaves (Fig. 270), the whole surface being beset with spines and large glandular hairs. The leaves were separated by long internodes and produced occasional axillary branches, whilst the stem was attached to the soil by a number of adventitious roots arising near its base. The microsporangia and megasporangia (ovules) were borne on the ultimate ramifications of the ordinary foliage-leaves (cf. Fig. 272).

The *stem* underwent considerable secondary thickening. In transverse sections (Fig. 271) the parenchymatous pith, which included patches of sclerotic tissue, is seen to have been surrounded by five or more groups of primary wood (*X.*), some of which occurred in pairs; in each such strand of primary xylem the protoxylem occupied a more or less central position. Beyond was a prominent zone of secondary wood (*Sec.*), with wide parenchymatous rays, through which the leaf-trace bundles emerged (*Bs.*). The delicate cells of the cambium and phloem, external to the

[1] See the works of D. H. Scott and A. C. Seward, cited on p. 386. A valuable presentation of the successive floras of the past will be found in A. C. Seward, *Plant Life through the Ages*. Cambridge Univ. Press, 1931 (601 pp.).

wood, are rarely well preserved. A layer of cork-like tissue (*periderm*) was usually developed in the pericyclic region, whilst

FIG. 270. The foliage of *Lyginopteris oldhamia* (formerly known as *Sphenopteris hœninghausii*). (From a drawing, after Potonié, lent by Prof. F. W. Oliver, F.R.S.)

the thin-walled inner cortex contained numerous secretory cells. A sharp contrast is afforded by the outer cortex, with its system of radial sclerenchymatous plates (*S.*), anastomosing at frequent intervals and giving mechanical support to the stem. In surface

sections these appear as a network in which the meshes are lozenge-shaped, hence their irregular spacing as seen in transverse sections.

Each *leaf* was supplied by one of the primary xylem strands which, as it passed outwards, became associated with phloem and, on entering the pericycle, divided into two. The double bundle (Fig. 271, *Bs.*) traversed several internodes before bending out into the leaf, whose detailed structure was much like that of many of

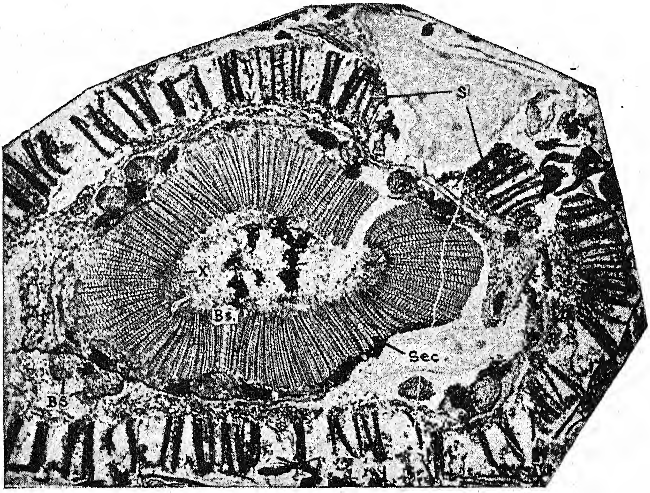


FIG. 271. Photograph of transverse section of the stem of *Lyginopteris oldhamia* (reproduced by the courtesy of Prof. F. W. Oliver, F.R.S.). *Bs.*, leaf traces; *S.*, sclerenchyma plates in outer cortex; *Sec.*, secondary wood; *X.*, primary xylem strand.

the simpler Ferns. The root was similar to that of recent plants, possessing from two to eight xylem-groups.

The *microsporangia* of *Lyginopteris* were borne on pinnæ, with much reduced laminæ. The pinna, with its elongated sporangia, had somewhat of the appearance of an epaulet (Fig. 272). The sporangia produced numerous small spores, which were presumably conveyed by the wind to the ovules, where they became lodged within the pollen chamber. Of their further fate nothing is known, but it is probable that they developed a small male prothallus, giving rise to spermatozoids, somewhat like those of Cycads.

The *ovules* arose singly from the ends of short branches of the fronds, and showed the same plan of construction as in Cycads (Fig. 274), except that each possessed, in addition to the integument, a second protective covering. This took the form of a lobed cup-like structure (*Cu.*), comparable with the cupule of

a Hazel-nut, and beset with the same glands as occur on the vegetative organs of *Lyginopteris* (cf. Fig. 273). The robust integument (Fig. 274, *I.*) was fused with the nucellus (sporangium-wall, *n.*), except for the apical portion, which was pierced by the narrow canal-like micropyle.

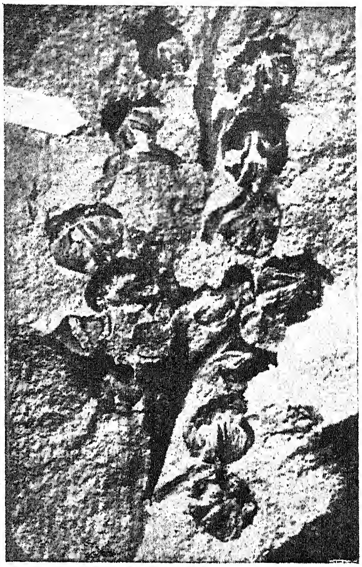


FIG. 272. Ultimate pinnules of the foliage of *Lyginopteris oldhamia*, with microsporangia. (From a photograph by the late Dr. R. Kidston, F.R.S.)

The tip of the nucellus was produced into a flask-shaped *pollen chamber* (*Pc.*), whose neck projected very slightly beyond the micropyle (cf. Fig. 273), so that the microspores reached the nucellus direct, a point of contrast to Cycads and most Seed Plants. The central portion of the pollen chamber was occupied by a dome of parenchymatous tissue, but between it and the surrounding wall was a narrow chink-like space (Fig. 274, *Pc.*) in which the pollen presumably germinated and liberation of the sperms ensured. The single huge megaspore (*m.*) has been found filled with a uniform thin-walled prothallus, which bore the archegonia near its apex. The seed was supplied by a single vascular strand, which gave off branches to both envelopes. Those traversing the cupule (Fig. 274, *Vb.*) extended into its lobes, whilst those running in the integument (*I.b.*) penetrated to the neighbourhood of the micropyle, where the integument became free from the nucellus.

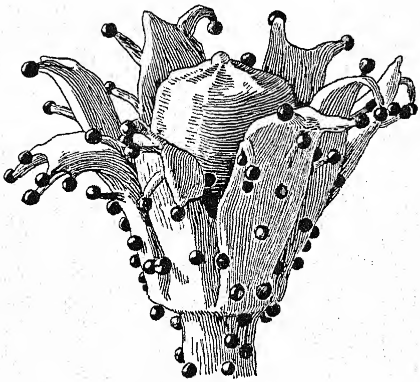


FIG. 273. Restoration of the seed (*Lagenostoma lomaxi*) of *Lyginopteris oldhamia*, in its glandular cupule. (After Oliver.)

The recent plants described in this chapter are especially characterised by

the method of fertilisation and the possession of seeds. As regards the former feature, the only essential difference from *Selaginella* lies in the germination of the microspores in close proximity to the megaspore, for which special devices such as the mucilaginous pollination drop and the pollen chamber are created. Moreover, with the help of the pollen tube, some nourishment is obtained from the adjacent nucellus.

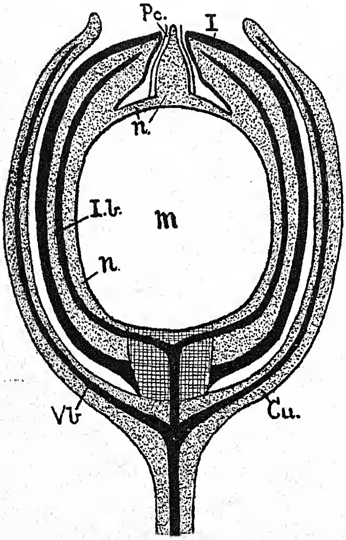


FIG. 274. Reconstruction of a longitudinal section through the seed of *Lyginopteris oldhamia* (after Oliver). *Cu.*, cupule; *I.*, integument; *I.b.*, bundle traversing integument; *m.*, megaspore; *n.*, nucellus; *Pc.*, pollen chamber; *Vb.*, bundle traversing cupule.

The *seed* may be looked upon as an extreme development of heterospory. Even in *Selaginella* it was noted that in some species there may be reduction to a single megaspore, which is retained within the sporangium till after fertilisation. Such reduction and retention are eminently characteristic of the seed-habit, where dehiscence of the megasporangium is dispensed with. The added protection, furnished by the integument, admits of a change in the character of the sporangium-wall, which becomes a thin-walled tissue serving as intermediary between the vascular system of the ovule and the developing megaspore and female prothallus.

The possession of a vascular system, another characteristic of the ovule, facilitates nutrition and the storing up of food-reserves for the young embryo. It is probably in consequence of the increased food-supply that ovules and seeds in general attain so large a size as compared with the sporangia of lower plants. As a general rule (*e.g.* most Conifers and Flowering Plants), however, the vascular system of the ovule stops short at its base. The elaborate vascular supply of the early seed-types, as contrasted with the more modern ones, may perhaps be related to the possession of motile spermatozoids, and to the relative degree of exposure and size of the ovules.

One important aspect of the permanent retention of the megaspore, involving considerable economy, is the possibility of post-

poning the accumulation of food-reserves to a relatively late stage, when fertilisation has taken place and the embryo has begun its development. The embryo is, moreover, more adequately protected, during its early phases, than is possible in Pteridophyta and Bryophyta, and, after attaining a certain stage, remains dormant and securely shielded until conditions arise suitable for its further growth.

CHAPTER XXXIV

THE CONIFERS

ALL seed-plants, with the exception of certain fossil forms (*e.g.* some fossil Clubmosses), are grouped as Spermaphyta. The subdivisions of this class, viz. Gymnosperms and Angiosperms, are characterised by the manner in which the ovules are borne; those of the former are not enclosed, whilst those of the latter, the Flowering Plants proper, are surrounded by a structure called the ovary. There are, however, other points of contrast, which will become apparent later. The Spermaphyta as a whole are further distinguished by a greater differentiation of the strobili than is found among Pteridophyta.

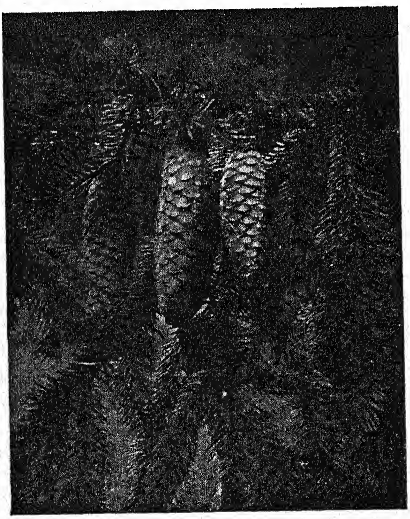


FIG. 275. Branches of the Spruce Fir (*Picea excelsa*) with three ripe cones. [Photo. E. J. S.]

The *Gymnosperms* include, apart from the Cycads, the Maidenhair Tree (*Ginkgo biloba*, cf. p. 400), the important group of the Conifers, and other forms known only as fossils. The Conifers, to which belong such familiar plants as the Scot's Fir (*Pinus sylvestris*, Fig. 285), Larch (*Larix europæa*, Fig. 276), Yew (*Taxus baccata*, Fig. 284), etc., are essentially characteristic of temperate zones, some being the chief forest trees of colder regions (cf. p. 485). They furnish some of the most important sources of timber (p. 181), turpentine, resin, etc. (p. 91). There are some 350 known species, of which more than a fifth belong to the genus *Pinus*.

All the Conifers [1] are woody, and the majority are trees. The regular habit, so marked in the Spruce Fir (*Picea excelsa*) and Cypress (*Cupressus*), characterises the group and is an outcome of the monopodial branching (cf. p. 116). The feature which gives them their most distinctive stamp, however, is the foliage, which in general consists of small needle-like *leaves* (Figs. 275, 276 and 284). These usually persist for several years, although the Larch, for instance, is deciduous.

The needles are either borne on the ordinary long shoots (*e.g.* Yew, Fig. 284, A, and Silver Fir), or, as in several common genera (*Pinus*, *Larix*, *Cedrus*, all members of the Abietineæ), are restricted to special *dwarf-shoots*. These arise in the axils of scale-leaves on the long shoots (Fig. 285), and bear a few dark-coloured scales below and a variable number of foliage leaves above. In the Pines the number of the latter is limited (five in *Pinus strobus*, two in *P. sylvestris*, Fig. 283, and only one in *P. monophylla*), and no further leaves are produced after the first season, the whole dwarf-shoot being shed at the end of two or three years. On the other hand, in the Larch (Fig. 276) and Cedar (*Cedrus*), where the dwarf-shoots are larger and bear a tuft of needles, quite a considerable number of new leaves is formed annually, although after some years this production ceases and the dwarf-shoots die away. These two Conifers also differ from the Pines in the fact that the needles are not entirely confined to the dwarf-shoots, since, during the first season's growth, they occur on the long shoots also. It will be realised that only the normal shoots contribute to the permanent branch-system of the trees.

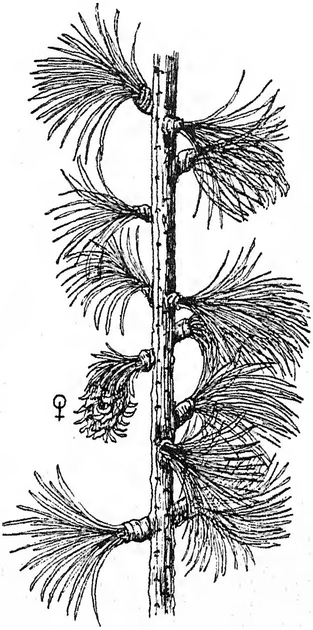


FIG. 276. Branch of the Larch (*Larix*), showing several dwarf-shoots, one of them bearing a young female cone. (Both about natural size.)

The leaves are most frequently sessile, although those of the Yew have a short stalk (Fig. 284, A). Their bases are often fused with the stem for a short distance, and persist after the leaves have fallen, leaving characteristic scars (*e.g.* Spruce Fir, *Picea*); in the

[1] For reference-books, see p. 425.

Scot's Fir similar scars are left by the shedding of the dwarf-shoots.

The peculiar appearance of the Arbor Vitæ (*Thuja*, Fig. 277) and the Cypress (*Cupressus*), both belonging to the Cupressineæ, is due to the presence of minute leaves arranged in decussate pairs, and almost fused with the stem upon which they are borne. Moreover, owing to the larger size of the lateral leaves, and the restriction of most of the branches to their axils, the shoot as a whole acquires a

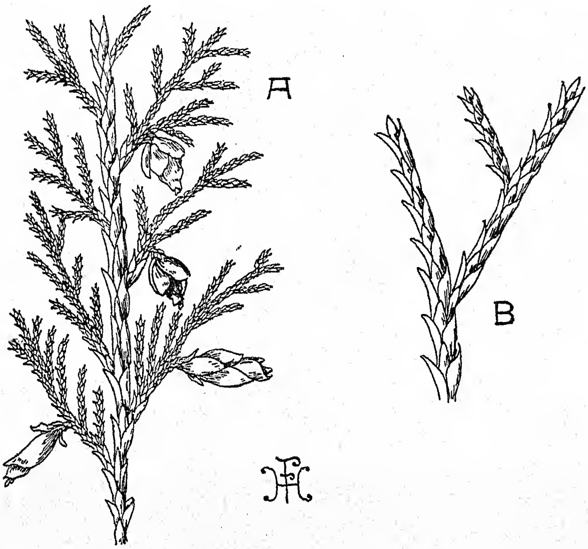


FIG. 277. Arbor Vitæ (*Thuja*). A, Branch with ripe female cones (about natural size). B, Small part of a branch enlarged to show the leaf-arrangement.

flattened appearance. In the common Juniper (*Juniperus*), which is likewise one of the Cupressineæ, three needle leaves arise at each node, and such a whorled arrangement is characteristic of this whole family. Large flattened leaves are seen in *Araucaria*, and a similar type of foliage is found in *Podocarpus*, which is the most important genus of Conifers in the Southern Hemisphere, comprising some sixty species, of which several furnish valuable timber.

In spite of the considerable diversity in the mature structure, the *seedlings* of most Conifers exhibit great uniformity, the young stem bearing ordinary needle-leaves for some little distance above the cotyledonary node (Fig. 278). The dwarf-shoots of *Pinus* and other Abietineæ, as well as the scale-like leaves found in the Cypress, etc., only appear at a later stage. The juvenile foliage sometimes persists, even in the adult condition, as in some cultivated varieties

of *Thuja* and *Cupressus* (the *Retinospora* of nurserymen). Even the deciduous habit of the Larch appears as a secondary acquisition, since in the seedling the leaves persist for some time. It is not always that the varied specialisation which a group has undergone,

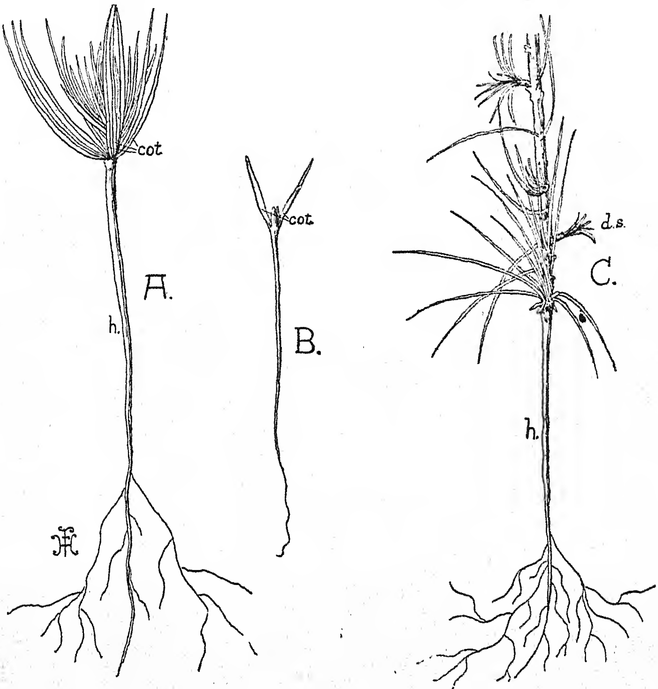


FIG. 278. Seedlings of various Conifers. A, *Pinus sylvestris*. B, *Cupressus*, showing two cotyledons and plumule. C, *Larix*, older seedling which has already produced several dwarf-shoots. *cot.*, cotyledons; *d.s.*, dwarf-shoot; *h.*, hypocotyl.

in evolving from a common ancestral type, is as plainly decipherable as in the Conifers.

The appearance of the *stem* in transverse section is very similar to that of a Dicotyledon having secondary growth. *Pinus* affords a typical example (Fig. 279, A). The irregular outline is due to the adherent bases of the scale-leaves which are occupied by a large-celled tissue (Fig. 279, B), on whose inner side the cork-cambium (*ca.*) arises. With the production of cork, therefore, the epidermis (*e.*) and the dwarf-shoots become exfoliated, so that the older branches have a relatively smooth surface. The narrow cortex is rather lacunar, and contains schizogenous *resin-canals* (*r.*)

(cf. p. 93). These resin canals are particularly characteristic of Conifers (Fig. 279, C), and are found in all parts of the plant.

The primary and secondary vascular tissues are not easily distinguished from one another, particularly in the *phloem*, the broad zone of which is chiefly secondary in origin. This tissue (*ph.*) is strikingly uniform, its elements, which have thick white shining walls, exhibiting a radial arrangement. The rows of more

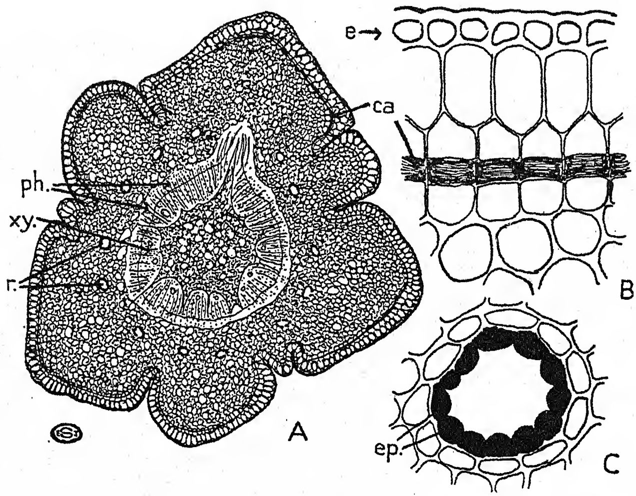


FIG. 279. Structure of the young stem of *Pinus sylvestris* in transverse section. A, Entire (diagrammatic). B, Small part of the peripheral tissues enlarged. C, Single resin-canal enlarged, showing the epithelium (*ep.*). *ca.*, cork cambium; *e.*, epidermis; *ph.*, phloem; *r.*, resin-canals; *xy.*, xylem.

or less empty-looking *sieve-tubes*, which have no companion cells, are interspersed with a smaller number of irregular files of phloem-parenchyma, whose cells contain dense contents. In longitudinal sections the sieve-tubes appear as long tapering elements bearing sieve-areas (Fig. 280, E, *Si.*) upon their sloping radial walls.

The secondary *wood* (Fig. 279, *xy.*), internal to the narrow cambial zone, also exhibits a very uniform, radially seriated structure. Except for the narrow parenchyma rays and occasional resin-canals, it consists entirely of fibre-like *tracheids*, which are differentiated among themselves only in respect of the distinctions between spring- (Fig. 280, A, *Sp.*) and summer-wood (*Au.*) [1] (see p. 177). The radial walls of the tracheids bear a single row of large circular bordered pits, especially evident in radial longitudinal (Fig.

[1] Annual rings are, however, absent from some *Araucarias*, and from most of the fossil representatives of this group.

280, C, *b*.) sections, when the pits themselves are seen in surface view. In the summer-wood the tangential walls are also pitted. The groups of primary xylem, composed of spiral tracheids, project into the small pith and are separated from one another by the primary rays.

The stem-structure of *Pinus* is typical of most Conifers, but

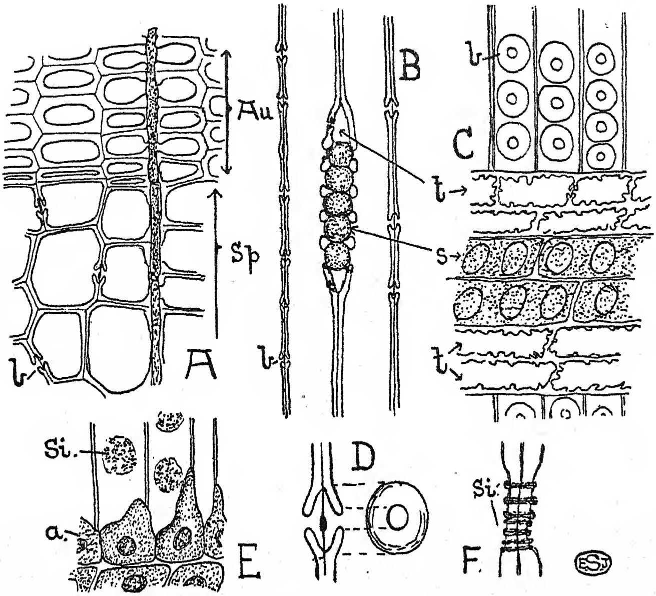


FIG. 280. Structure of the stem of *Pinus sylvestris*. A, Small part of the secondary wood in transverse section, showing spring- (*Sp.*) and summer- (*Au.*) wood; B, The same in tangential longitudinal section showing a parenchyma ray; C, The same in radial longitudinal section, with part of a parenchyma ray; D, Single bordered pit in section (on the left) and from the surface (on the right); E, Small part of the secondary phloem in radial longitudinal section; F, Single sieve-tube in tangential longitudinal section. *a*, marginal cells of parenchyma ray of phloem; *b*, bordered pits; *s*, storage cells of rays; *Si.*, sieve-plates; *t*, tracheidal cells of rays.

resin-canals are absent from the wood in certain genera (being often replaced by resin-cells), whilst in the *Araucarias*, and occasionally in other members of the group (e.g. *Pinus palustris*), the tracheids bear two or more rows of bordered pits. Resin-canals are lacking in *Taxus*.

Radial and tangential longitudinal sections exhibit the same arrangement of the *parenchyma rays* as in Dicotyledons (Fig. 280). In some Conifers certain rays, which are relatively wide, are traversed by resin-canals connecting those of the pith and cortex.

As a general rule the rays consist of uniform cells, whose walls usually bear simple pits. Several Abietineæ, including *Pinus*, show a complex differentiation of the rays, best seen in radial longitudinal sections. In the region of the wood the cells of the middle rows, which bear simple pits of exceptionally large size, are more particularly concerned with storage, and contain copious starch (Fig. 280, C, *s.*); the dead and empty cells of the marginal rows (*t.*), which bear small bordered pits and often exhibit peg-like ingrowths of the walls, have a conducting function. Where the rays traverse the phloem, all the cells have thin walls and dense cytoplasm, but those at the margin (Fig. 280, E, *a.*) are often drawn out into finger-like processes which are insinuated between the sieve-tubes.

The *root*, which is generally diarch, shows the usual structure, although characterised by the presence of a large resin-canal within each protoxylem-group.

The *leaves* of most Conifers are traversed by a single vein only, but, apart from that, their structure is somewhat varied. Its range can, however, be gauged from a consideration of the relatively simple dorsiventral leaf of *Taxus* (Fig. 281) and the more complex centric one of *Pinus* (Fig. 282). In the former the epidermis (Fig. 281, *ep.*) shows the thick cuticle and sunken stomata (Fig. 281, B) associated with transpiration-reduction; the pronounced papillæ on the lower surface (Fig. 281, B, C) are a special peculiarity. The mesophyll, comprising two layers of palisade cells (*p.*) and spongy tissue (*s.*), is traversed by the single bundle (*b.*), which exhibits the usual dorsiventral structure. On either side of the xylem, however, are occasional spirally or reticulately thickened elements (*t.*), which sometimes bear bordered pits. These dead cells constitute what is called *transfusion tissue*, and may serve both for the lateral conduction of water, thus compensating for the absence of side-veins, and as water-reservoirs.

The epidermal cells of the *Pinus*-leaf (Fig. 282, A, B) also have a very pronounced cuticle (*Cu.*), and are so strongly thickened that their cavity is often reduced to a mere dot (*ep.*); beneath the epidermis is a strongly thickened hypoderm (*h.*). The deeply sunken stomata (*St.*) occur at intervals all round a transverse section, but, if the leaf be examined with a lens, they are seen to be arranged in longitudinal rows. The mesophyll contains several prominent resin-canals (*r.*) and consists of more or less isodiametric cells, characterised by the presence of inwardly projecting folds of the wall (*i.*). As seen in transverse section it will be noticed that, apart from the respiratory cavities of the stomata, there are few intercellular spaces in the mesophyll. This tissue, however, con-

sists of successive transverse lamellæ, which are separated from one another by narrow air-spaces (Fig. 281, E). The twin-bundles are connected by a group of thick-walled mechanical

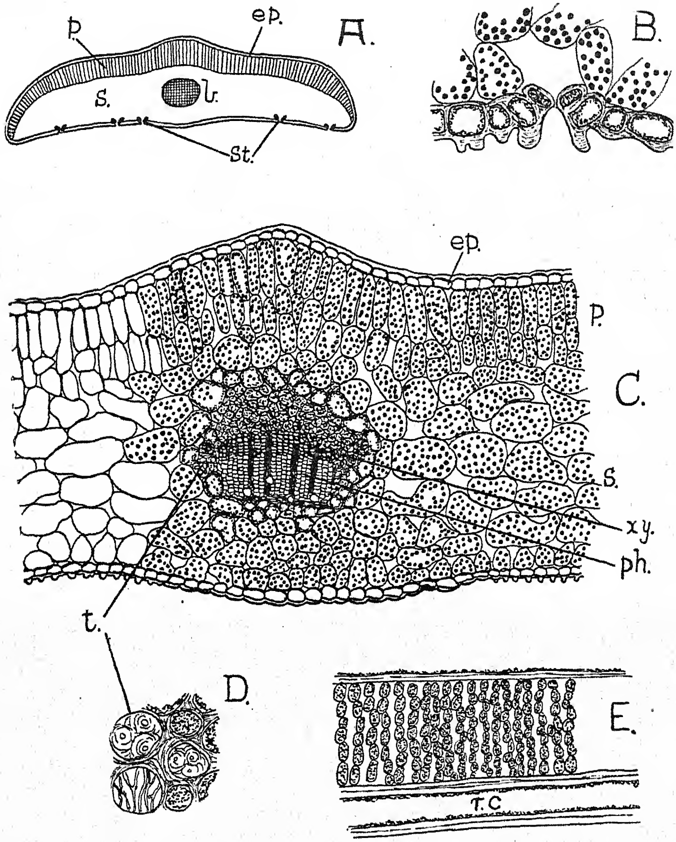


FIG. 281. A–D, Structure of the leaf of *Taxus baccata* in transverse section. A, Diagram of whole section; B, Single stoma enlarged; C, Central part; D, A few cells of the transfusion tissue. *b.*, bundle; *ep.*, epidermis; *p.*, palisade tissue; *ph.*, phloem; *s.*, spongy tissue; *St.*, stomata; *t.*, transfusion tissue; *xy.*, xylem. E, Tangential longitudinal section of leaf of *Pinus*, showing a resin-canal (*r.c.*) and the transverse lamellæ of photosynthetic cells.

cells (Fig. 282, A, D, *Scl.*) and are embedded in an extensive mass of tissue bounded by a well-marked bundle-sheath (*S.*). This tissue consists, in large part, of ordinary living parenchymatous cells containing starch-grains. Scattered among these are the dead and empty cells of the transfusion tissue (cf. especially Fig. 282, C, *tr.*),

bearing small bordered pits (*b.*), which are seen both in section and from the surface. At the outer edge of the phloem of each bundle is a group of cells, whose dark contents are rich in proteins (*a.*). In some species of *Pinus*, as well as in *Picea* and *Larix*, the leaf contains but a single bundle.

Whilst many of the features of Coniferous leaves are those

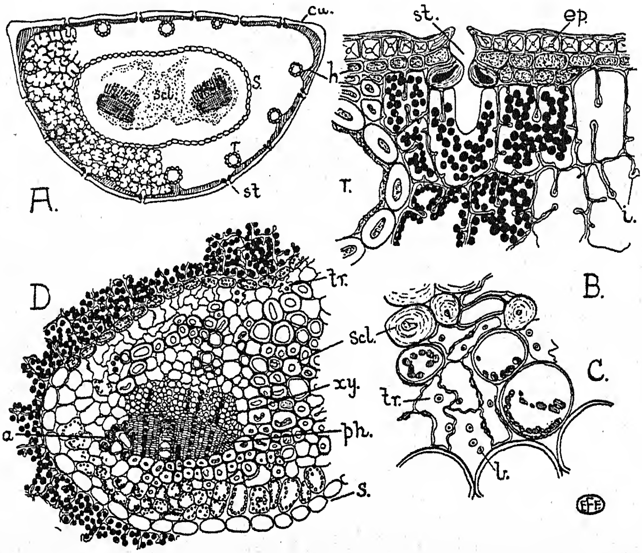


FIG. 282. Structure of the leaf of *Pinus* in transverse section. A, Diagram of whole section. B, Small part of the superficial tissues, enlarged. C, A few cells of the transfusion tissue, etc., from the central vascular cylinder, greatly enlarged. D, About half the central vascular cylinder. *a.*, protein cells; *b.*, bordered pit on transfusion cell; *Cu.*, cuticle; *ep.*, epidermis; *h.*, hypoderm; *i.*, folds on walls of mesophyll-cells; *ph.*, phloem; *r.*, resin-canal; *S.*, bundle-sheath; *Scl.*, sclerenchyma; *st.*, stomata; *tr.*, elements of transfusion tissue; *xy.*, xylem.

usually found in plants which require to economise their water-supply, others such as the limited vascular supply and the transfusion tissue are special peculiarities of the group. The relation between the vascular system of stem and leaf in Conifers is similar to that which obtains in Flowering Plants (cf. p. 168).

The sporophylls of Conifers, like those of Cycads, are grouped in cones (Fig. 283, 285), the two kinds being most commonly found on the same plant, though *Taxus* (Fig. 284), for instance, furnishes an exception. The *male cones*, which often occur in clusters (Fig. 283), are yellow oval structures of diverse size, and frequently arise in the axils of the foliage-leaves (e.g. *Taxus*, Fig. 284, E;

Abies). In *Pinus*, where they are axillary to scale-leaves, the male

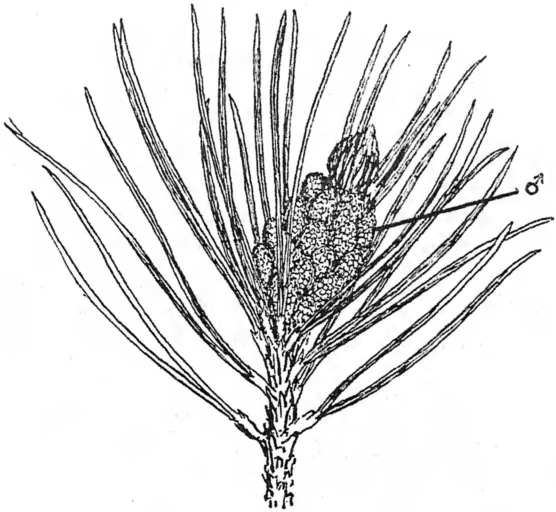


FIG. 283. Portion of a branch of *Pinus*, bearing male cones (♂) on the lower part of the year's growth (natural size). Near the top of the latter are seen, closely crowded, a number of immature dwarf-shoots.

cones replace the dwarf-shoots (Fig. 283), but in the Larch, for instance, the latter bear leaves below the male cones.

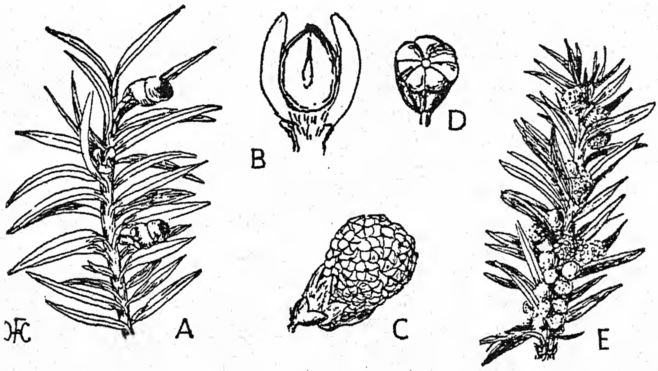


FIG. 284. *Taxus baccata*. A, Branch bearing two ripe seeds; B, A ripe seed in longitudinal section, showing the aril; C, Single male cone, enlarged; D, Single microsporophyll; E, Branch with male cones. (D, after Eichler; the rest original.)

The axis of the male cone (Fig. 286, A) supports large numbers of densely crowded microsporophylls, which mostly have the form

of flattened scales, whose upturned overlapping tips are alone visible at the surface. They usually bear two large microsporangia (*pollen sacs*) on their under-surface (Fig. 286, B, *ps.*), although there are sometimes several (e.g. *Cupressus*). In *Taxus* the stamens are peltate in form, with several (5 to 9) pollen sacs pendant from the lower side of the lamina (Fig. 284, D). In *Araucaria* also the microsporophylls bear numerous (10 to 20) pollen sacs.

The young microsporangia are provided with a wall of several layers which encloses large numbers of spore mother-cells, each dividing in the customary manner to form four haploid microspores (*pollen grains*). The pollen sacs usually dehisce by means of a broad split, and the pollen is distributed by the wind. In *Pinus* and its allies the microspores develop a pair of blister-like enlargements, between the cuticle and the inner layer of the membrane; these contain water, which subsequently evaporates, thus leaving two bladders which act as wings (Fig. 288, A, *w.*).

The *ovules* (megasporangia) of the Yew (*Taxus*) usually occur singly within small buds, which arise in the axils of the leaves; they closely resemble the ordinary vegetative buds. Each bears several minute scales, the single ovule occupying a terminal position with the micropyle facing outwards. The ovule is peculiar in possessing, apart from the usual integument, a second protective covering termed the *aril*, which remains inconspicuous till after fertilisation. It then develops into a bright-coloured fleshy cup investing the seed (Fig. 284, A, B; Fig. 338, D–F).

In most Conifers, however, more or less numerous ovules are found within each of the *female cones*, and these in the Monkey Puzzles (*Araucaria*), for instance, may attain considerable dimensions. The cones themselves occupy diverse positions. Thus, in *Pinus* (Fig. 285) they first appear as small reddish structures, situated at the ends of short stalks, just beneath the apical bud of the current year's growth. In the Larch, where they are larger and of a bright crimson colour, they terminate some of the dwarf-shoots, with a rosette of green needles at their base (Fig. 276). The small cones of the Cypress and Arbor Vitæ (Fig. 277, A) occupy a similar position.

The scale-like sporophylls generally show a spiral arrangement, although in *Cupressus* and *Thuja* they are decussate, like the foliage-leaves. In *Pinus* and other Abietineæ (*Larix*, *Abies*, etc.) the axis of the cone bears two different types of scales which are quite distinct from one another, and occur in superposed pairs (Fig. 286, D). The lower or bract scale (*bs.*) of each pair is smaller than the upper or ovuliferous scale (*Os.*). The latter appears to arise in the axil of the former, and bears, on its upper surface, two

ovules (*Ov.*) whose micropyles face towards the axis of the cone (Fig. 286, E). The difference in size becomes more pronounced

FIG. 285. Branch of *Pinus* bearing female cones of two ages (about one-half natural size). *d.s.*, dwarf-shoot; *s.l.*, scale-leaf.

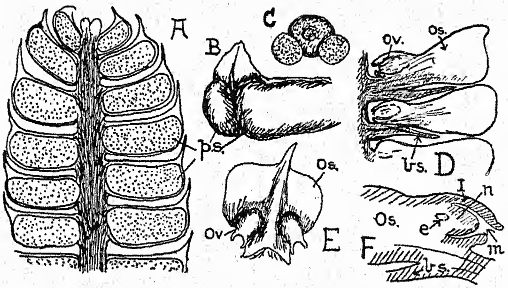


FIG. 286. A–B, Structure of male cone of *Pinus sylvestris*. A, Upper part in longitudinal section; B, Single sporophyll. *ps.*, pollen sacs. C, Pollen grain. D, Longitudinal section of female cone of *Pinus*. E, Single megasporophyll, from above. F, Part of D, enlarged. *bs.*, bract scale; *e.*, megaspore; *I*, integument; *m.*, micropyle; *n.*, nucellus; *Os.*, ovuliferous scale; *Ov.*, ovule.

as the cone grows older, the ovuliferous scale enlarging to a much greater extent than the bract scale. In the Wellingtonia (*Sequoia*,

Fig. 289, D) and Cupressineæ bract and ovuliferous scales are almost completely joined, whilst in some Conifers (e.g. *Cryptomeria*) the line of fusion is plainly recognisable. The scales in the Cupressineæ usually bear more than two ovules, situated with the micropyles directed outwards; not infrequently the uppermost

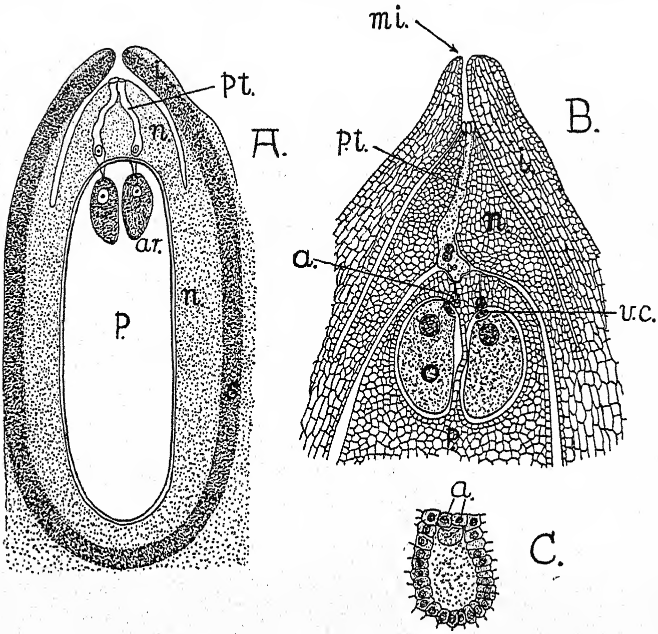


FIG. 287. Structure of Ovule of *Pinus*. A, Diagrammatic longitudinal section of mature ovule (after Coulter and Chamberlain). B, Front portion of same greatly enlarged, showing a pollen tube penetrating the nucellus (after Strasburger). C, Young archegonium showing the layer of nutritive cells investing the egg (after Ferguson). *a.*, neck of archegonium; *ar.*, archegonium; *i.*, integument; *mi.*, micropyle; *n.*, nucellus; *o.*, egg; *p.*, female prothallus; *p.t.*, pollen tube; *s.*, stony layer of integument; *v.c.*, ventral canal cell.

scales are sterile (e.g. *Thuja*). The Monkey Puzzles are peculiar in having but a single ovule on each megasporophyll.

The *ovules* in most Conifers possess a single thick integument (Fig. 286, F, *I*; Fig. 287, *i.*). This is partially fused on one side with the ovuliferous scale (Fig. 286, F), and, except in a few genera, the central nucellus is only free from the integument in the region of the micropyle (Fig. 287, B, *mi.*). A single megaspore (*p.*) is usually differentiated within the nucellus of the young ovule by the division of a mother-cell which arises hypodermally. This forms a linear tetrad of potential haploid spores of which only the inner-

most survives. The functioning spore rapidly enlarges and eventually displaces the greater part of the nucellus, though a pronounced cap of tissue still remains in the free portion beneath the micropyle (Fig. 287, *n.*). The thin-walled parenchymatous *female prothallus* (*p.*), which is richly supplied with food-material, as a rule arises only after pollination has occurred. The archegonia (*ar.*), which are usually few in number (*e.g.* three in *Pinus sylvestris*), are generally differentiated at the micropylar end. Each consists of a huge ovum (*o.*) embedded in the tissue of the prothallus, a minute ventral canal cell (*v.c.*), and a very short inconspicuous neck (*a.*) composed of one or more tiers of cells. When the archegonia are numerous (as in most Cupressineæ) they are usually collected together in groups, opening into a common shallow depression (*archegonial chamber*), at the front end of the prothallus.

When the mature pollen is being scattered broadcast by the wind, the axis of the female cone elongates slightly, so that the cone-scales spread apart, thus giving access to the ovules. The mature pollen grains are caught on micropylar lobes of the integument which act like stigmas. At night a fluid secretion fills the micropylar canal and entraps the grains. By the gradual shrinking of the fluid the pollen grains are sucked through the micropyle on to the surface of the nucellar cap, and, soon after this, the scales of the female cone enlarge and once again fit tightly together. In *Taxus* the fluid exudes from the micropyle as a drop which receives the pollen grains direct. This process of *pollination* must be sharply distinguished from that of fertilisation which occurs at a later stage—often only after a prolonged interval.

When shed, the contents of the microspores have already undergone division, the cell, or cells, thus cut off from the general body lying against one side of the grain (Fig. 288, B); usually there is only an *antheridial* cell (*a.c.*), but in *Pinus* and related forms its formation is preceded by the cutting off of two very flat cells, which soon break down (Fig. 288, B, *v.c.*). The remaining and larger portion of the pollen grain forms the so-called tube cell (*t.n.*). On reaching the nucellus the outer membrane of the microspore is ruptured, and the tube cell grows out to form the *pollen tube* (Fig. 287, *p.t.*), into whose tip its nucleus wanders, whilst simultaneously the antheridial cell divides into two, the inner half (*body cell*) subsequently forming the two male cells.

The growth of the pollen tube into the nucellus soon ceases, and is not resumed till a short time before fertilisation. This interval between pollination and fertilisation is comparatively short (four to six weeks) where the seeds mature in the same year as that in which pollination occurs (e.g. *Thuja*, *Picea*), but is very

prolonged (twelve to thirteen months) in the Pines, where pollination ensues in May or early June, whilst the seeds are not shed till the autumn of the following year. In the latter there is very pronounced growth of the female cones and ovules in the interval between pollination and fertilisation (cf. Fig. 285).

With the resumption of growth the pollen tube penetrates

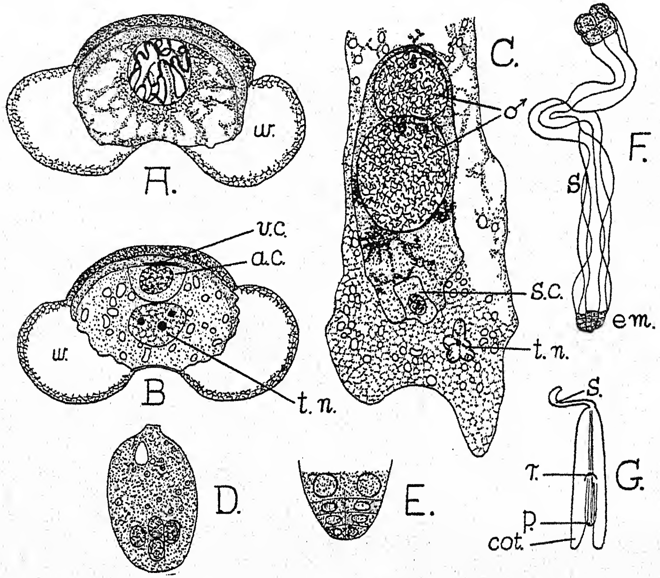


FIG. 288. Pollen and embryology of *Pinus*. A, Mature pollen grain, nucleus not yet divided; B, Pollen grain at time of pollination; C, Lower end of pollen tube a little before fertilisation. *a.c.*, antheridial cell; *s.c.*, stalk cell; *t.n.*, tube nucleus; *v.c.*, vegetative cell; *w.*, wing of pollen grain; ♂ (in C), the two male nuclei. D–G, Embryology. D, Fertilised ovum, with nucleus divided into four: E, Lower end of oospore, showing young pro-embryo; F, Much older pro-embryo; G, Almost mature embryo. *cot.*, cotyledon; *em.*, embryo; *p.*, plumule; *r.*, radicle; *S.*, suspensor. (A–D after Ferguson; the remainder after Strasburger.)

deeper into the nucellus (Fig. 287, *p.t.*), frequently exhibiting slight lobing, and the two naked *male cells*, resulting from the division of the body cell, pass down into its apex (Fig. 288, C, ♂). On reaching an archegonium the neck is crushed, and the pollen tube, breaking open at its tip, discharges its contents into the ovum. Subsequently one of the two male nuclei fuses with the egg-nucleus. In *Pinus* the second male nucleus is smaller (Fig. 288, C) and usually aborts, though in some genera (*e.g.* of Cupressineæ), where the archegonia occur in groups and the pollen tube discharges into

the common archegonial chamber, both the male nuclei, which are here of equal size, may function.

The fertilised egg, becoming enveloped in a delicate membrane, almost immediately exhibits two successive divisions of its nucleus (Fig. 288, D). The four nuclei thus formed wander to the end of the egg remote from the micropyle, where they become grouped in a single plane. Further division, accompanied by the formation of separating walls, ultimately results in the development of three or four superposed tiers (Fig. 288, E), each usually consisting of four cells and occupying only a small part of the oospore. In the *proembryo* of *Pinus* the tier farthest from the micropyle gives rise to the new plant,[1] whilst the cells of the adjacent tier elongate very considerably (Fig. 288, F, *S.*) and form a *suspensor* (cf. *Selaginella*, p. 395), which carries the developing *embryo* (*em.*) down into the middle of the prothallus.

The cells of the embryonic tier divide repeatedly to form an extensive mass of tissue. At the end away from the micropyle a number of lobes soon grow out and form the cotyledons (Fig. 288, G, *cot.*). These surround the developing plumule (*p.*), whilst the radicle (*r.*) arises as a pointed structure at the opposite end, adjacent to the suspensor (*S.*). The number of cotyledons is very variable; there are only two in *Taxus* and Cupressineæ (Fig. 278, B), whilst in *Pinus* (Fig. 278, A) there are from three to seventeen, according to the species.

As the embryo enlarges it absorbs the food-reserves stored up in the prothallus and gradually displaces it. At the time when the *seed* is fully mature, however, a considerable part of this tissue still persists unaltered around the embryo and constitutes the *endosperm* (Fig. 289, A, *e*); the seed of Conifers is thus endospermic. The food-reserve is largely of the nature of oil, and is present in sufficient quantity to render the kernels of some species of Pines of nutritive value. The method of germination of the seeds is practically the same as that of a Castor Oil, the seedlings (Fig. 278) possessing long hypocotyls (*h.*) with epigeal cotyledons (*cot.*).

During the development of the embryo the entire ovule enlarges considerably, and at the same time the integument hardens to form the seed-coat, or *testa* (*s.*). The greater part of the latter comes to consist of very thick-walled tissue, foreshadowed as a dark zone in the integument of a young *Pinus*-ovule (Fig. 287, A, *s.*), and constituting the hard layer which is so conspicuous a feature in the seed of the Stone Pine (*Pinus pinea*). The micropyle appears

[1] In *Pinus* and some other genera the cells of the pro-embryo commonly separate, and as many as eight embryos may be formed, but, as in other Conifers, one only reaches maturity.

on the testa as a minute opening, and it will be realised, from the foregoing description, that the tip of the radicle lies just beneath this. In *Pinus* and some of its allies, a thin membranous flake becomes detached from the ovuliferous scale and adheres to the ripe seed, forming a wing which aids in dispersal by the wind (Fig. 289, E, *w*.). In *Cephalotaxus* and a few other genera the ripe seeds are plum-like, resembling those of Cycads.

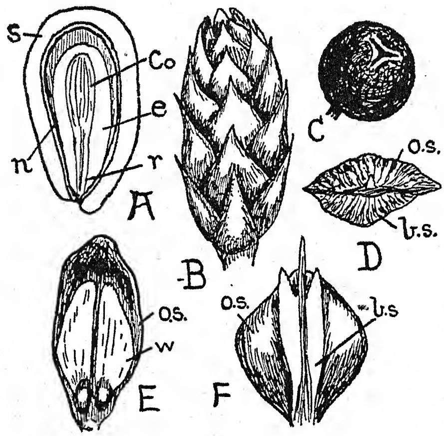


FIG. 289. Seeds and cones of various Conifers. A, Longitudinal section of ripe seed of *Pinus pinea*, showing testa (*s*), perisperm (*n*, cf. p. 471), endosperm (*e*), and embryo with radicle (*r*) and numerous cotyledons (*Co*.); B, Young female cone, and C, Ripe cone of *Juniperus*; D, Outer edge of ripe cone-scale of *Sequoia*; E, Single cone-scale of *Pinus* bearing the two seeds with wings (*w*); F, Ripe cone-scales of *Pseudotsuga*. *b.s.*, bract scale; *o.s.*, ovuliferous scale. (B, after Antoine.)

The cones also undergo considerable enlargement in ripening, often becoming many times larger than they were prior to fertilisation (Fig. 285). The ripe cone-scales are usually woody, and gape apart to set free the seeds, although in the Cedar, for instance, they are shed with the latter. At this stage the bract-scales in *Pinus* are no longer recognisable, though in some of the related forms (*e.g.* the Douglas Fir, *Pseudotsuga douglasii*, Fig. 289, F), they are conspicuous even in the mature cone. The Juniper is peculiar in that the cone-scales become fleshy, forming a berry-like structure (Fig. 289, C) in which the ripe seeds are embedded; the seeds are here distributed by birds.

In the life-history of the Conifers the method of fertilisation shows a considerable advance on that of Cycads, since the pollen tube, which is there but an organ for the absorption of nourish-

ment from the nucellus (a function which it may also fulfil to a slight extent in the Conifers), is here utilised to convey the motionless male cells to the egg. Thereby the necessity for the presence of liquid water at the time of fertilisation is rendered unnecessary.

[For a more detailed treatment of Gymnosperms, see J. M. Coulter and C. J. Chamberlain, *Morphology of Gymnosperms*, Univ. Chicago Press, 2nd edit., 1917 (466 pp.); and W. Dallimore and A. Bruce Jackson, *A Handbook of Coniferæ*, Ed. Arnold, 2nd edit., 1931 (582 pp.). For taxonomic works, see p. 578.]

CHAPTER XXXV

FLOWER-STRUCTURE

THE majority of the Angiosperms, the second subdivision of the Spermaphyta, are easily distinguished from the Gymnosperms by the possession of *flowers*, which are really highly specialised fertile shoots. In some, however, the flowers are relatively inconspicuous (*e.g.* Grasses), and scarcely conform to the popular notion of such structures. The Angiosperms are more markedly characterised by the enclosure of their ovules in a protective ovary, as well as by the possession of true vessels and of sieve-tubes of a special type (cf. p. 62).

The classification of Angiosperms into *Monocotyledons* and *Dicotyledons* is based on many morphological and anatomical features (leaf-form, number of cotyledons in the embryo, stem- and root-structure, and number of floral parts), the Monocotyledons being an essentially herbaceous group exhibiting a high perfection of means for perennation and hibernation (*e.g.* bulbs, corms, etc.). The evidence that the Dicotyledons and Monocotyledons were derived from a common stock is almost overwhelming. This fact is plainly indicated, for example, by the widespread traces of the presence of a cambium in Monocotyledons, and the extremely few characters, either of development or structure, that are entirely restricted to the one or the other group (cf. also p. 446).

The Angiosperms are the predominant vascular plants on the earth's surface at the present day, and comprise upwards of 150,000 species. In Britain this preponderance is especially marked. The native Angiosperms here number about 1500 species and the Gymnosperms 4 species; amongst the Cryptogams there are about 60 Pteridophyta, 600 Mosses, 250 Liverworts, several thousand species of Algæ, and at least 5000 species of Fungi. The Angiosperms first appear in the geological succession in the Cretaceous period,[1] but the study of these and of the abundant

[1] For further details on fossil Angiosperms, see L. Laurent, *Les Progrès de la paléobotanique angiospermique, etc.*, Progressus Rei Bot., I, 1917, p. 319 *et seq.*

Tertiary fossils, though affording much that is of interest, has so far shed no light whatsoever on the origin of the group, which is merged in obscurity. The details of the life-history betray a very high degree of specialisation, but afford practically no evidence as to how this has been attained.

The physiological activities of the Angiosperm may be said to culminate in the formation of flowers and seeds. The manner in which the flowers are borne is often of biological significance and sometimes characterises entire families or genera. Sometimes the flowers are solitary (Fig. 296), but more commonly a number occur together on a flower-bearing shoot termed the *inflorescence*. This exhibits one of the two types of branching found in the vegetative parts (cf. p. 116), or more rarely both types occur together. If the branching is monopodial the inflorescence is termed *racemose*,[1] if sympodial it is termed *cymose*. Each flower usually arises in the axil of a leaf (except in Cruciferæ), which often differs markedly from the foliage-leaves and is termed a *bract*. The bracts show much morphological resemblance to bud-scales. The ultimate branches of the inflorescence end in flowers, and their stalks (*peduncles*) often bear one or two scale-like leaves termed *bracteoles*. A flower-bud may arise in the axil of a bracteole so that the bracteole of one flower becomes the bract of a younger one.

Racemose inflorescences (Fig. 290, A) are characterised by the flowers opening from below upwards. Cymose inflorescences exhibit a reverse order of opening of the flowers (Fig. 290, G), from above downwards or, if flat-topped (cf. below), the oldest flowers are towards the centre. The growth of any axis in a cymose inflorescence is terminated by the production of a flower which opens before those on the lateral branches below.

The chief types of *racemose inflorescence* are: The simple raceme (Fig. 290, A), in which each flower is stalked (*e.g.* Currant, Lupine); the compound raceme (Fig. 290, D), where the branches are themselves racemes (*Festuca*); the corymb (Fig. 290, B), a simple raceme in which the lower peduncles become increasingly longer so that the flowers approximate to the same level (Candytuft, *Iberis*, Fig. 316); the spike (Fig. 290, E, and 291), a simple raceme with sessile flowers (*Plantago*, Fig. 313). Simple racemes and spikes, in which the internodes are not recognisable, are respectively termed umbels (*e.g.* Cowslip, Fig. 290, C) and capitula (*e.g.* Daisy, Dandelion, Fig. 290, F, and 312, A). In the corymb, umbel, and capitulum the opening of the flowers appears as from without inwards.

In most Umbelliferæ we have examples of compound umbels. Catkins are loose spikes in which the flowers contain either stamens or an ovary only (*e.g.* Hazel, *Corylus*, Fig. 314).

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[1] For the definition of this and other terms, see the work of Jackson cited on p. 123.

The chief types of *cymose inflorescence* are: The simple cyme (e.g. *Geum*, Fig. 290, G), found in plants with alternate leaves; the dichasial cyme (e.g. *Lychnis*, Fig. 290, H), in plants with opposite leaves. The dichasial cyme appears forked below each of the older flowers, but one of the branches of the ultimate pairs is often suppressed. Cymose umbels (*e.g.* Onion), cymose capitula (*e.g.* Scabious), and cymose corymbs (*e.g.* Wayfaring tree, *Viburnum*) also occur.

Richly branched inflorescences often exhibit a racemose development of the main axis and laterals, whilst the ultimate branches develop in a cymose manner

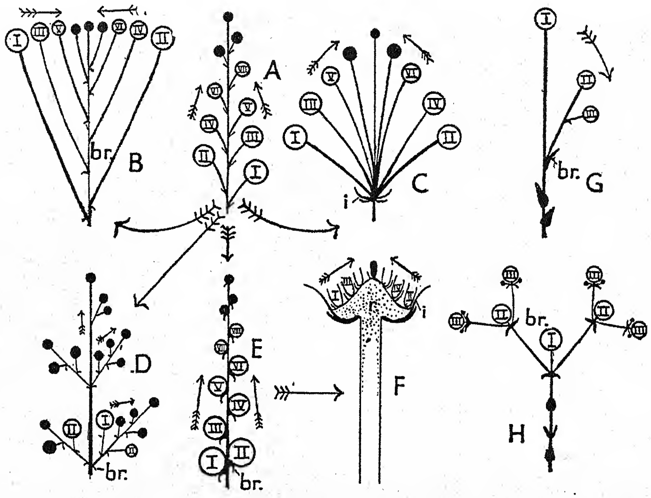

FIG. 290. A–F, Diagrams of different types of racemose inflorescences. A, Simple raceme. B, Corymb. C, Simple umbel. D, Compound raceme. E, Spike. F, Capitulum. G, H, Diagrams of cymose inflorescences. G, Simple cyme. H, Dicharial cyme The Roman numerals, as well as the small arrows, indicate the order of opening of the flowers. The larger arrows show the relation of the different types to one another. *br.*, bracts; *i.*, involucre; *r.*, receptacle.

(e.g. *Æsculus*, *Syringa*). In the Labiatæ the axillary groups of flowers are dichasial cymes, but those at the base are the oldest and those at the tip the youngest.

The massing of small flowers into an inflorescence renders them more conspicuous. In very condensed types, such as capitula, the numerous bracts form a whorl or whorls at the base of the inflorescence, known as an *involucre*, and collectively constitute a protective investment (Fig. 290, F, *i*).

The individual flower is a compressed shoot, serving for purposes of reproduction and bearing a number of different structures which are usually not separated by internodes. Of these floral organs some are essential for the production of seed (stamens and ovary),

whilst others constitute the non-essential *perianth* (calyx and corolla) which, however, mostly plays an important part in the protection of the flower and in the attraction of insect-visitors. When the flower, as in the Ash, contains only the essential organs it is said to be *naked* (Fig. 291).

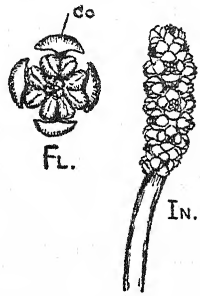

Fig. 291. Flower (*Fl.*) and inflorescence (*In.*) of *Potamogeton* (the flower enlarged, inflorescence natural size). *co.*, connective.

The expanded end of the peduncle to which the different floral organs are attached is spoken of as the *receptacle* or *thalamus*. This is frequently more or less convex in form, bearing at its summit the ovary, with stamens and perianth (or corolla and calyx) at successively lower levels. Such flowers, in which the other parts arise from beneath the ovary, are said to be *hypogynous* (*e.g.* Buttercup, Fig. 293, A, and Hyacinth, Fig. 294, B). Occasionally the receptacle is flattened, and from this it is but a slight step to one which is more or less deeply concave (Fig. 292, B and C); examples are furnished by *Potentilla* (Fig. 292, C) and *Rosa* (Fig. 292, B), which show progressive hollowing out of the thalamus, so that the central ovary (which in the former is situated on a central protuberance)

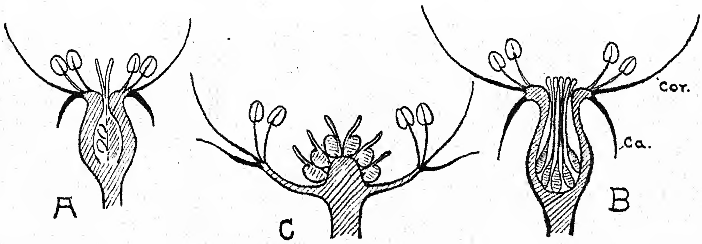

Fig. 292.—Diagrams to show different types of floral receptacle. A, Apple (epigynous flower). B, Rose (extreme perigynous type). C, *Potentilla* (perigynous flower). Receptacle shaded in all cases. *Ca.*, calyx; *Cor.*, corolla.

becomes more and more enclosed. Such flowers are described as *perigynous*. If the ovary becomes completely enveloped and altogether joined up with the receptacle (Fig. 292, A), whilst the remaining floral organs arise from its top, the flower becomes *epigynous*, as in the Umbelliferæ (Fig. 315, E) and Narcissus (Fig. 293, B). In the Apple (Fig. 292, A) ovary (core) and receptacle (flesh) are clearly distinguishable. In these flowers the

ovary is situated below the other organs, *i.e.* is *inferior*, whilst in peri- and hypogynous flowers it is *superior*.

In those flowers, which for many reasons are regarded as relatively unspecialised (*e.g.* Ranunculaceæ and its allies), the floral receptacle is elongated,[1] bearing sepals, petals, stamens, and carpels at successively higher levels, and these parts are wholly or in part spirally arranged; the stamens and carpels, moreover, are usually numerous, and not joined in any way. The further evolution and specialisation of the flower has brought about increased efficiency and precision in pollination, and appears to have involved a gradual shortening of the floral receptacle, with the result that the different sets of organs became whorled and reduced in number. At the same time fusion of parts may take place to a more or less marked extent. Another development appears to have been concerned with the better protection of the ovary, the receptacle gradually becoming more and more concave (progressive stages can be found in the perigynous Rosaceæ), until the flower is epigynous. Certain it is that the most highly specialised families (Umbelliferæ, Compositæ, Orchidaceæ) all possess such epigynous flowers, with the different members in whorls. Further specialisation is connected with the development of irregular flowers (p. 456).

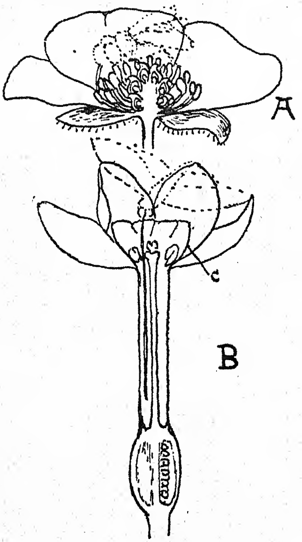

FIG. 293. Vertical sections of flowers of A, Buttercup (open type); B, Pheasant's-eye Narcissus (tubular type), showing hypogyny and epigyny respectively. The body of the pollinating insect is shown by dotted lines, the proboscis being indicated by a continuous line. *c*, corona.

The features hitherto considered are best illustrated by means of *longitudinal sections* through the middle of the flower, as in Fig. 292. In drawing such sections it is advisable to show only the actual cut surface (cf. Fig. 294, B). The section should faithfully represent the shape of the receptacle, as well as the position of attachment of the floral organs, and should indicate the orientation of bracts and bracteoles with reference to the flower.

Apart from the longitudinal section, a *floral diagram* or ground-plan of the

[1] Extreme elongation of the floral receptacle is seen in *Myosurus* and *Ranunculus sceleratus*. In whorled flowers local development of internodes may occur, as between calyx and corolla (*Silene inflata*) or between corolla and stamens (*Passiflora*).

flower is necessary to complete the picture of its structure (cf. Fig. 294, A). The main axis (*m.a.*), on which the flower is borne, is shown by a dot and after that the exact position of the different floral whorls, as well as of the bracts and bracteoles, with reference to the main axis and to one another, is indicated (as in Fig. 294, A and C–F); all the members arising at one level are placed on the same circle and the ovary is shown in cross-section. The side of the flower adjacent to the axis of the inflorescence is *posterior*, whilst that away from it is

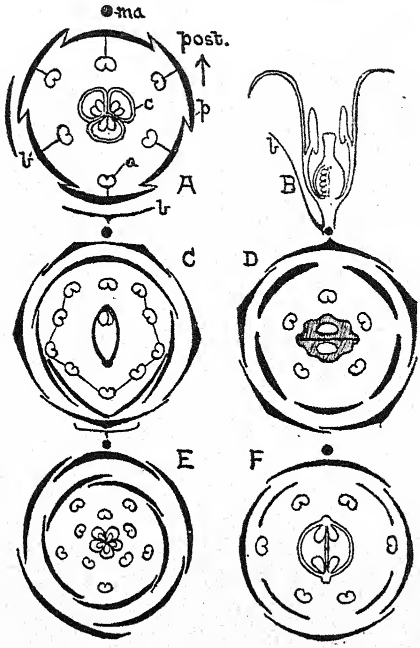

FIG. 294. Diagrams of floral structure. A and C–F, Floral diagrams. A, Hyacinth (Liliaceæ). C, Sweet-pea (Leguminosæ). D, Hogweed (Umbelliferæ). E, Geranium. F, Wallflower (Cruciferæ). *a*, stamen; *b*, bract; *b'*, bracteole; *c*, ovary; *m.a.*, main axis; *p*, perianth-member; *post.*, posterior side of flower. B, Longitudinal section of flower of Hyacinth, taken through the median plane. *b*, bract.

anterior. A longitudinal section which passes from the posterior to the anterior side of the flower passes through the *median plane* and is the customary one for longitudinal sections.

The floral diagram of the Hyacinth (Fig. 294, A) shows that all the different whorls have their parts in threes; this is found in many Monocotyledons and such a flower is said to be *trimerous*. On the other hand, *Geranium* (Fig. 294, E), a Dicotyledon, has its parts in fives and its flower is consequently described as *pentamerous*, a type of frequent occurrence in the latter group, although flowers with their parts in fours (i.e. *tetramerous*, as in *Epilobium*, Fig. 311), or twos (e.g. *Circæa*, Fig. 427, C, D), are also found.

The normal flower of both Monocotyledons and Dicotyledons has two whorls of perianth-members (Fig. 294). In Monocotyledons (Fig. 294, A) the

main axis lies opposite the interval between two members of the outer whorl—that is to say, the third member is anterior, whereas in most Dicotyledons the odd (fifth) member of the outer perianth-whorl is situated opposite the axis—in other words is posterior (Fig. 294, D and E). In the Leguminosæ (Fig. 294, C), however, the odd sepal is anterior. In general the members of one whorl alternate with those of the next and this is always so in the perianth. In Dicotyledons, however, it is not uncommon for the outer whorl of stamens to stand opposite the petals (e.g. *Geranium*, Fig. 294, E). The number of whorls, moreover, varies in the flowers of different plants; apart from the absence of a perianth (*e.g.* Ash, see p. 429), there may be only one whorl of stamens (*e.g.* Umbelliferæ, Fig. 294, D) or more than two (*e.g.* Rosaceæ). In the Hyacinth (Fig. 294, A) and *Geranium* (Fig. 294, E) the same number of parts occurs in each whorl, but this is by no means the general rule, the ovary frequently consisting of less (two in Umbelliferæ, Fig. 294, D; one in Leguminosæ, Fig. 294, C), and not uncommonly this is true also of the stamens (e.g. *Veronica*, with a tetramerous perianth and two stamens, Fig. 430, B).

The two alternating *non-essential whorls*, when alike in colour and texture (*e.g.* most Monocotyledons), are termed a perianth. In Dicotyledons, on the other hand, as well as in some Monocotyledons (*e.g.* Water Plantain *Alisma*, Fig. 441, B), the outer whorl is generally green and protective, whilst the inner one is brightly coloured and attractive, and we then speak of a *calyx* and *corolla* respectively. Occasionally there is only one perianth-whorl, which is then generally green, and good examples of such *apetalous* flowers are furnished by the Stinging Nettle and Dog's Mercury (Fig. 295).

FIG. 295. Apetalous, unisexual flowers of the Dog's Mercury (somewhat enlarged). The left-hand one is the male, the right-hand one the female.

The individual sepals of the calyx are with rare exceptions green in colour. Their protective character is well seen in most flower-buds in which all the inner parts are completely enveloped by the sepals. The sepals may actually drop off as the flower expands (*e.g.* Poppy, Fig. 163, *c*) and the necessity for protection becomes less urgent. As a general rule, however, the calyx is *persistent* and may subsequently, long after the petals and stamens have withered, afford protection to the fruit (*e.g.* Campion, Mallow, Fig. 334, C).

The necessity of the calyx as a protective envelope is easily demonstrated by carefully removing it from a number of young buds (*e.g.* Poppy) without damaging the rest of the flower; as a result the latter will be found either to dry up or to show half-withered petals when it expands.

Sometimes bracteoles grade off into the perianth, as in the Lesser Celandine in which the outer members (actually modified bracteoles) are green and may even exhibit a reduced lamina similar to that of

the foliage-leaves. Thus the protective sepals of the reproductive bud or flower may be compared with the scale-leaves which protect the foliage-bud. In the Winter Aconite (Fig. 296) the functions of the calyx are performed by three much-divided bracteoles closely resembling the foliage-leaves and arising immediately beneath the coloured perianth. This recalls the state of affairs seen in the Wood Anemone in which, however, the three bracteoles are situated some little way below the flower.

FIG. 296. Flower of the Winter Aconite (*Eranthis*) (natural size), showing the three divided bracteoles which function as a calyx.

We have likened the flower to a compressed shoot, and this analogy is emphasised by certain abnormal flowers, such as the Double Arabis; here, instead of producing essential organs the axis continues to grow, forming a series of successive flowers with short separating internodes, the one within the other and each consisting only of calyx and corolla.

The sepals are usually simple in form and either arise quite separately from one another (*polysepalous*, Geranium, Fig. 294, E, and Wallflower, Fig. 317) or are more or less completely joined to form a tube with free tips corresponding to the component members (*gamosepalous*, Fig. 297, B and C, shown by joining edges of sepals in floral diagram, cf. Fig. 422, C). When the individual lobes of a gamosepalous calyx are of the same size it is said to be *regular* (Henbane, Fig. 297, B), but frequently owing to unequal development an *irregular* calyx is produced (*e.g.* the two-lipped calyx of many Leguminosæ, Fig. 320, A and B); less commonly a polysepalous calyx shows irregularity, as in the Garden Nasturtium (Fig. 297, A) in which one side is produced into a long *spur*. Where the flowers are closely massed together in the bud, so that they afford one another mutual protection, the calyx is often greatly reduced. Thus, in the Umbelliferæ it merely forms a green rim, whilst in the capitula of Compositæ, in which additional protection is afforded by the involucre, the leaf-like character of the sepals is altogether lost; the calyx here generally consist of a circle of hairs (the *pappus*, Fig. 297, E, *p*) which aid in fruit-dispersal (cf. p. 480).

The *petals* of the corolla in Dicotyledons and of the perianth in Monocotyledons exhibit a great variety of form, developing either separately (*polypetalous*, Buttercup, Fig. 293, A, and Tulip) or being more or less joined together so as to form a corolla-tube with free lobes (*gamo-* or *sympetalous*, Primrose,

Fig. 318, and Narcissus, Fig. 293, B). Free petals are usually much larger than the sepals and very commonly have an entire margin (Fig. 293, A; Fig. 298, B),

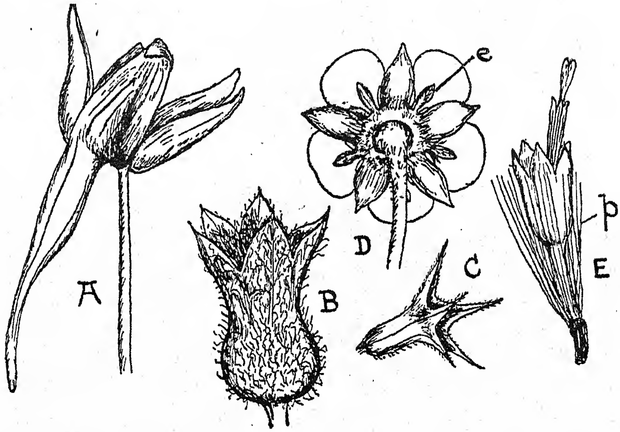

FIG. 297. Forms of calyx (A–D natural size, E enlarged). A, *Tropæolum* (spurred). B, Henbane (*Hyoscyamus*) (gamosepalous). C, *Lamium* (gamosepalous and slightly irregular). D, *Geum*. *e*, epicalyx. E, Tubular floret of *Aster* (Compositæ). *p*, pappus.

although sometimes more or less deeply divided (*e.g.* Fig. 422, A and B). As a general rule the petal has only an extremely short stalk (Fig. 298, B), but occasionally (*e.g.* Pink, Fig. 298, A, Wallflower) the blade terminates a long claw (*cl.*) with which it forms almost a right angle.

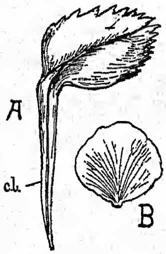

FIG. 298. Forms of petals (about two-thirds natural size). A, *Dianthus*. B, *Geum*. *cl*, claw.

The sympetalous corolla shows considerable diversity of form (cf. Fig. 299). The corolla, like the calyx, may be *regular* or *irregular*; examples of the latter condition are furnished by the *bilabiate* corolla of the Labiatæ (Fig. 299, D). An irregular corolla may, however, also occur amongst polypetalous forms, as for example, the butterfly-shaped (*papilionaceous*) corolla of the British Leguminosæ (Fig. 320) and that of Orchids (Fig. 326).

In the bud the sepals either fit edge to edge (*i.e.* are *valvate*, as in *Clematis*) or more commonly overlap (*i.e.* are *imbricate*, as in the Buttercup; cf. also Fig. 294, C–E). Since the space within the flower-bud is as limited as in a vegetative bud, the developing petals become folded just as do the young foliage-leaves (cf. p. 129). Most commonly the petals overlap one another, so that their arrangement is *imbricate* (Fig. 294, C and E); more rarely a crumpled folding (Poppy, Fig. 163, *b*) or a twisted arrangement (*Gentiana*, Fig. 300, A and C) obtains.

In the same way as outgrowths, such as stipules and the ligule of Grasses (p. 126), have been found arising at different points from foliage-leaves, so also analogous structures occasionally develop in relation to the calyx and corolla. Thus, in some plants leafy processes develop between the bases of adjacent

sepals, so that there appear to be two alternating whorls of the latter, the outer of which is then spoken of as an *epicalyx* (*e.g.* Strawberry; *Geum*, Fig. 297, D, *e*; Mallow). Similarly tubular corollas may produce outgrowths, usually near the

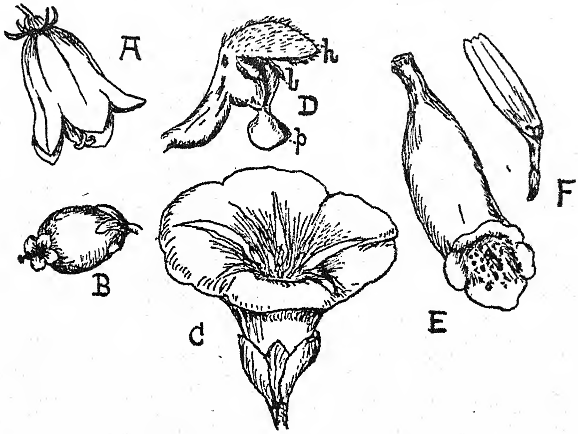

FIG. 299. Forms of gamopetalous corolla (all natural size). A, *Campanula*. B, *Erica*. C, *Convolvulus*. D, *Lamium* (bilabiate). *h*, upper lip (hood); *l*, side-projections; *p*, lower lip (alighting platform). E, *Digitalis*. F, Ray-floret of Compositæ (ligulate).

top of the tube, which either arise independently from each petal (*e.g.* the teeth-like processes of the Campion) or form a united fringe (Fig. 300, B and D, *co.*), or a complete membranous tube (the *corona* of Daffodil and Narcissus, Fig. 293, B, *c*).

The sequence of development of the floral parts is usually from without inwards, viz. calyx, corolla, stamens, ovary. Each *stamen* (Fig. 302, A) consists of a stalk or filament (*f*) and a swollen pollen-producing part or *anther* (*a*). The latter exhibits two lobes joined by a continuation of the filament known as the *connective*. The stamens are microsporophylls and comparable to foliar structures bearing marginal sporangia (the pollen sacs). The lamina is represented by the connective. The foliar nature of the stamen is indicated where the connective is developed as a flat petal-like structure (as in *Potamogeton*, Fig. 302, B, *Co.*), or where stipule-like outgrowths arise from the bases of the filaments (*Allium*, Fig. 302, C).

Most commonly the anther is rigidly attached to the filament (Fig. 301, A, C, and F), but occasionally (as in Grasses, Fig. 301, D) it is more or less loosely suspended from its end.

Sometimes appendages develop on the anthers (e.g. *Calluna*, Fig. 301, E, *ap.*) or rarely the connective branches (*e.g.* Sage, Fig. 322, E). In the Violet (Fig. 325, B, *c*) the connective forms a membranous prolongation beyond the anther.

If more than one whorl of stamens is present, the individual whorls usually

alternate with one another (Fig. 294, A and E). The outermost stamens commonly alternate with the inner series of perianth-leaves, but in the Primrose (Fig. 429) the five stamens are situated opposite the petals, whilst in *Geranium* (Fig. 294, E) the outermost whorl occupies a similar position. When the stamens are numerous, they are often spirally arranged, as in the Buttercup (Fig. 423), and their number is usually very variable; we then speak of them as

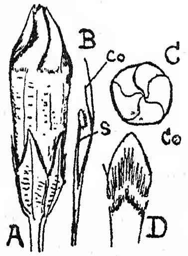

FIG. 300. Structure of flower of *Gentiana germanica* (natural size). A, Entire flower-bud, showing twisted arrangement of petals. B, Longitudinal section of petal, showing epipetalous stamen and corona. C, Petals in bud, seen from above. D, Single petal, showing corona. *co*, corona; *s*, stamen.

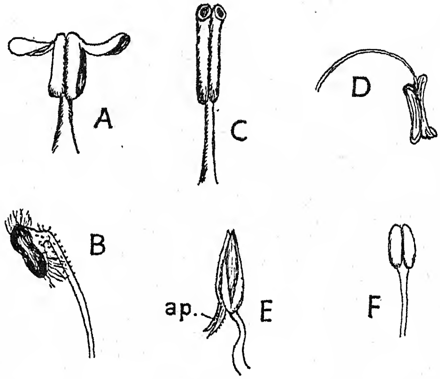

FIG. 301. Stamens and stamen-structure (all natural size). A, Bay-tree (*Laurus*), showing dehiscence. B, Dead-nettle. C, *Rhododendron*, showing dehiscence. D, Vernal Grass (*Anthoxanthum*). E, *Calluna*, showing dehiscence. *ap.*, appendages. F, *Ranunculus*.

indefinite. The stamens are most commonly of equal length, but many exceptions occur, *e.g.* four long and two short (*tetradynamous*, Cruciferæ, Fig. 424, A); two long and two short (*didynamous*, Labiatæ); five long and five short (*Stellaria*, Fig. 315, C). The stamens collectively constitute the *androecium*.

The number of stamens is often equal to, or some multiple of, the number of members in the perianth-whorls (Fig. 294, A and C–E). Exceptions are most usually found in flowers having only a single whorl of stamens and possessed of an irregular corolla, *e.g.* Labiatæ (Fig. 432) and Scrophulariaceæ (Fig. 430, C), in both of which there are generally only four stamens; other examples are furnished by *Veronica* (Fig. 430, B) and Rosemary (*Rosmarinus*) with only two, and *Tropæolum* with eight stamens. A careful study of the arrangement of the stamens in these flowers indicates that one or more have failed to develop, and confirmation is furnished by flowers in which a sterile structure or *staminode*[1] (not producing pollen) occupies the position of the missing stamen. This is well illustrated by the Figwort and *Pentstemon* members of the Scrophulariaceæ, in which the staminode (Fig. 310, *St.*) occupies the posterior position in the stamen-whorl (Fig. 430, C), which, in most other members of this family and of Labiatæ, is vacant. In the Stork's

[1] In the floral diagram this is indicated by a small circle or in the way shown in Fig. 430, C; missing stamens are marked by a dot (cf. Fig. 430, B).

Bill (*Erodium*), an ally of *Geranium*, there are five staminodes opposite the petals and five fertile stamens.

The stamens may either be free from one another or joined together in various ways. Thus, in *Genista* (Fig. 426, A) and Gorse the ten filaments are united for the greater part of their length (*i.e.* are *monadelphous*), so as to form a tube round the young pod. A somewhat similar condition is seen in the Mallow, where the numerous stamens have joined filaments. In the Compositæ (Fig. 312) and *Jasione* (Fig. 436, E), on the other hand, the five filaments are free, whereas the anthers are connected (*syngenesious*). Moreover, in many flowers with tubular corollas the filaments of the stamens are more or less completely fused with the petals (*epipetalous*, Fig. 294, B; 300, B), since they appear to arise from the latter. Finally it may be noticed that in a few flowers the stamens exhibit branching, those of the St. John's Wort (*Hypericum*), for instance, forming five bundles each dividing into numerous filaments bearing anthers.

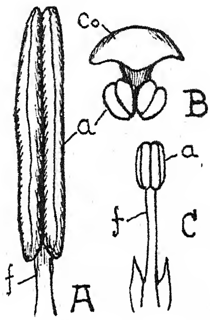

FIG. 302. Various forms of stamens. A, Tulip (ordinary form). B, *Potamogeton*, showing the enlarged connective (*Co.*). C, Onion (*Allium*), with stipular outgrowths from the base of the filament. *a.*, anthers; *f.*, filaments.

A single vascular bundle traverses filament and connective. The anther normally bears four *pollen sacs*,[1] two on either side of the connective (Fig. 303, A), although in the Mallow-family (Malvaceæ) the stamens bear but two pollen sacs. In transverse sections through immature flower-buds, the anthers are seen to consist of uniform thin-walled tissue bounded by a distinct epidermis, whilst a slight lobing foreshadows the future pollen sacs (Fig. 303, B). At a slightly later stage four subepidermal strips of varying width (often of only a single cell) become distinguishable, one in each lobe; these strips consist of cells with prominent nuclei and dense contents, and constitute the *archesporia* (Fig. 303, C, *a.*), each of which extends as a narrow band of tissue for almost the whole length of the anther. Each archesporial cell divides tangentially (Fig. 303, C), and, from the inner halves thus formed, the actual pollen-producing tissue arises, so that the *pollen mother-cells* are really subepidermal in origin. The outer half of each archesporial cell divides to form the wall of the pollen sac (Fig. 303, D), which thus consists of several layers.

In transverse sections through older anthers (Fig. 303, A), the mass of spore mother-cells in the centre of each pollen sac is seen to be surrounded by a nutritive layer (*tapetum*, *t.*). This is composed of large, often palisade-like, cells with prominent nuclei and

[1] For further details on the reproductive morphology of Angiosperms, see J. M. Coulter and C. J. Chamberlain, *Morphology of Angiosperms*. Appleton, New York, 1904 (348 pp.).

dense contents. Between the tapetum (*t.*) and the epidermis (*ep.*) of the anther are two or more layers, the outermost of which generally consists of rather large, subsequently thickened cells (*fibrous layer*, *f.*), whilst the others (*m.l.*) are usually very much flattened.

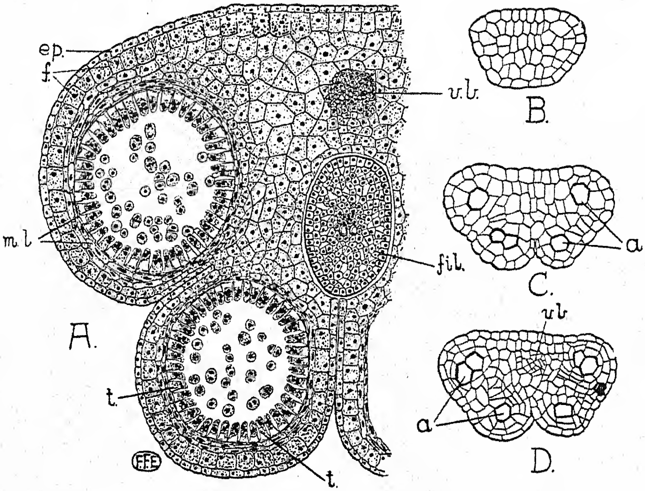

FIG. 303. Development of the anther. A, Section of part of anther of young stamen, showing the pollen sacs at the mother-cell stage (the mother-cells are seen in various stages of division). B, Section of young anther before the archesporia are differentiated. C and D, Later stages. *a.*, dividing archesporial cells; *ep.*, epidermis of anther; *f.*, fibrous layer; *fil.*, filament; *m.l.*, middle layers; *t.*, tapetum; *v.b.*, vascular bundle of connective. (A, original; the remainder after Warming.)

Each pollen mother-cell, as in the groups previously studied, undergoes two divisions (cf. Fig. 303, A), the first of which is the reduction division. The four *pollen grains*, thus formed within each mother-cell, generally fall apart as the membrane of the latter becomes dissolved. But in a few plants the members of each tetrad remain in connection, when the pollen is shed (e.g. *Typha*, *Neottia*, Fig. 304, D, *a–c*; Ericaceæ, Fig. 304, D, *d.*), and a more extreme condition is seen in Orchids, where all the pollen grains formed by the single stamen cohere as two masses or *pollinia* (Fig. 304, F). Such cohesion is, however, only met with in insect-pollinated flowers. During the development of the pollen grains the tapetum undergoes gradual disorganisation (Fig. 305, *t.*), prior to which the cells often become bi- or multi-nucleate.

The mature pollen grain possesses a wall of two layers, the outer of which is thick and cuticularised, whilst the inner is delicate. Where the pollen is wind- or water-borne, its surface is commonly

smooth and dry, but when conveyed by insects it is usually sculptured in various ways (Fig. 304, B, G) and covered with a sticky oil. The outer layer is perforated, or rendered thin, by one or more pores or pits (Fig. 304, C, *o.*), through one of which the pollen tube is subsequently protruded. In this respect the pollen of Angiosperms is more specialised than that of Gymnosperms, where the outer layer of the membrane merely bursts in germination.

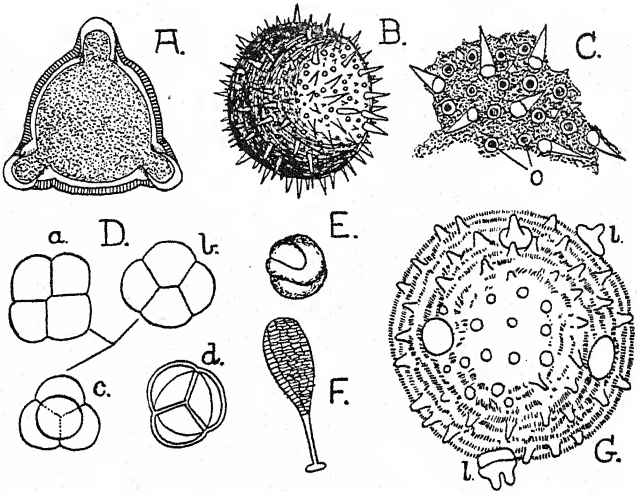

FIG. 304. Diverse types of pollen. A, *Epilobium*, with three thin spots in the outer coat. B, Hollyhock (*Althæa*), with numerous pores. C, Small part of same enlarged, showing the pores (*o.*). D, Pollen-tetrads, *a–c*, of *Neottia nidus avis*; *d*, of Bilberry (*Vaccinium myrtillus*). E, Musk (*Mimulus moschatus*). F, Pollinium of *Orchis morio*. G, Pollen grain of *Cucurbita pepo*, showing the embossed lids (*l.*) of the outer coat, which become pushed off by the growing pollen tubes. (A–D, after Sachs; *d* and F, after Wettstein; E, after Mohl; G, after Schacht.)

As the pollen matures the walls of the cells composing the *fibrous layer* become strengthened by radial bars of thickening which are often connected on the inner tangential walls, and simultaneously the cells lose their living contents (Fig. 305, *en.*); many of the cells in the region of the connective, moreover, develop similar thickenings. At this stage the two pollen sacs, in each half of the anther, become confluent through the drying up of the intervening thin-walled septa, and it is this same process of desiccation that ultimately leads to the setting free of the pollen. Drying is usually due to direct loss of moisture to the air, but may result from the withdrawal of water by neighbouring cells of high osmotic content, belonging either to nectaries (e.g. *Stellaria*, Fig. 315, C)

or to sugar-containing tissue (e.g. *Digitalis*); hence dehiscence of the stamens ensues, even in a saturated atmosphere.

Actual splitting usually takes place longitudinally, along the middle line of each anther-lobe; the line of weakness is sometimes bounded on either side by a spindle-shaped group of enlarged epidermal cells (*e.g.* Lily). The thickenings of the cells of the fibrous layer (Fig. 305, *en.*) prevent radial contraction, so that the tangential shrinkage brings the bars together like the closing of the hood of a perambulator; it is the tension thus set up that finally results in rupture. The edges of the slit, thus formed (Fig. 424, C), curl back, but in damp air they often bend forwards into their original position and so protect the pollen. According as the connective develops mainly towards the outer or inner face, the lines of dehiscence of the anthers are towards (viz. *introrse*; *e.g.* Umbelliferæ, Fig. 294, D), or away from, the centre of the flower (i.e. *extrorse*; *e.g.* Buttercup, Fig. 423). In a few flowers dehiscence takes place in other ways, as, for instance, by apical pores (Ericaceæ, Fig. 301, C, E), or by the formation of subapical valves which hinge backwards to allow the shedding of the pollen (*e.g.* Barberry) (cf. also Fig. 301, A).

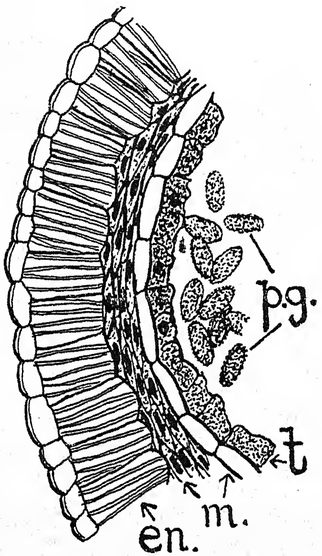

FIG. 305. Transverse section through part of a pollen sac of a ripe anther. *en.*, fibrous layer; *m.*, middle layers; *p.g.*, pollen grains; *t.*, disorganised tapetum.

The *ovary* of the Angiosperm consists of one or more *carpels* or *megasporophylls* which may either be joined together to form a *syncarpous* ovary (*e.g.* Liliaceæ, Fig. 294, A, *c*) or they are free (*apocarpous* ovary, Buttercup, Fig. 293, A; Fig. 306, C). The leaf-like structure of the carpels is best seen in ovaries of the latter type. Thus, in a young fruiting specimen of the Larkspur or Monkshood (Fig. 333, *b*) one margin of each carpel bears a prominent midrib (or *dorsal suture*, *m*), from which lateral veins (*l.v.*) are seen to arise; on the opposite margin there is a slight furrow, where the somewhat enlarged edges of the carpels are joined and form two *placentæ*, each bearing a row of ovules. It is along this line (the *ventral suture*) that the fruit subsequently opens. Except for the inrolling, such a

carpel might be compared to the megasporophyll of *Cycas* (cf. p. 398).

Similarly, if a young pod of a Pea be split lengthwise, it will be found to break more readily along the edge bearing the young seeds (*i.e.* the ventral suture); moreover, the latter are seen to occur on both valves, since some remain attached to one half and some to the other. In *Reseda* the margins of the carpels are not joined together, except at the base, even in the young ovary. The tip of each carpel terminates in the *stigma*, which is often borne on the end of a prolongation, the *style*.

In the syncarpous ovary the sides of adjacent carpels are more or less joined together. A slight fusion is seen in the Monkshood (Fig. 333, *b*) in which the individual carpels are frequently united at their bases by the ventral sutures. When the carpels are completely connected in this way, we obtain an ovary divided by *septa* into as many compartments or *loculi* as there are carpels, the structure being described as *bi-*, *tri-*, *quadri-*, or *multilocular* according to their number; thus the Umbelliferæ (Fig. 294, D) and the Scrophulariaceæ (Fig. 323, D) have a bilocular, the Hyacinth (Fig. 294, A) has a trilocular, the Willow-herb (Fig. 427, B) has a quadrilocular, and the Mallow a multilocular ovary. If only one carpel is present we have a *monocarpellary* ovary, as in Leguminosæ (Fig. 294, C).

A second mode of junction of the carpels in syncarpous ovaries is that in which the adjacent edges are united without the individual carpels being folded together, the ovary consequently having only one compartment (*i.e.* it is *unilocular*; *e.g.* Violet, Fig. 325, C). The ovary is then described as *bi-*, *tri-*, *quadri-*, or *multicarpellary* according to the number of component carpels, and this feature can be determined either by the character of the style and stigma or by the arrangement of the ovules.

Whatever the type of syncarpous ovary, the tips of the individual carpels are either free or more or less joined. Thus, in some ovaries the styles and stigmas are distinct (*e.g.* the St. John's Wort, Fig. 306, A) so that the number of component carpels is quite apparent. More usually, however, the styles of a syncarpous ovary are completely united to form a single structure, the stigma dividing into as many segments as there are carpels (*e.g.* three in *Campanula*, Fig. 306, F; two in Compositæ, Fig. 299, F). The stigma either divides into a number of narrow arms or is merely lobed. The actual sticky receptive surface (on which the pollen can alone germinate) is normally situated on the upper side. In the Primrose (Fig. 318), the stigma constitutes a small swelling (*capitate stigma*) at the end of the style. The almost flat top of the multicarpellary ovary of the Poppy (Fig. 333, *h*) bears a number of dark radiating lines which represent stigmas of a peculiar type.

When the edges of the carpels of a syncarpous ovary meet at the centre, the ovules are naturally situated on the central column (placenta), formed by the fused swollen margins of the carpels (Figs. 293, B; 294, B); the arrangement or *placentation* of the ovules is then said to be *axile* (*e.g.* Hyacinth, Fig. 294, A). When the ovary is unilocular, the ovules are borne in rows (frequently two) along the lines of junction of the carpels, so that we can speak of marginal or *parietal* placentation (*e.g.* Violet, Fig. 325, C). The number of placentas here again gives an indication of the number of carpels composing the ovary. In some plants the parietal placentas project more or less markedly into the cavity,

as for instance in *Hypericum* (Fig. 306, B). A third type of placentation is seen in the Caryophyllaceæ (*e.g.* Campion) and Primulaceæ (Fig. 318) in which the ovules are borne on a central upgrowth arising from the base of the ovary, a so-called *free central placenta*; in the former family septa are occasionally found connecting the placenta with the ovary-wall. In the White Water-lily (*Nymphæa*) and in the Flowering Rush (*Butomus*) the ovules arise in an unusual way from the whole inner surface of the carpels.

The number of ovules in the ovary, or in its individual compartments, varies considerably; thus, in the Scrophulariaceæ and Liliaceæ they are numerous, whilst there are but two in each loculus in the Sycamore, and one only in each

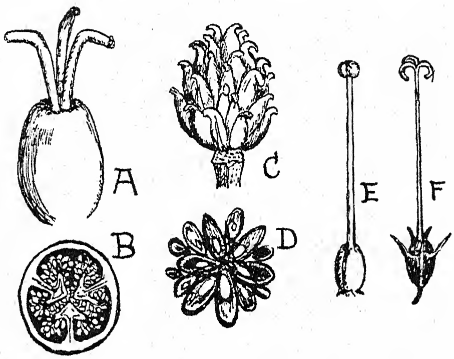

FIG. 306. Ovaries and ovary-structure (E and F natural size, the other figures enlarged). A, Ovary of *Hypericum*. B, The same in cross-section. C, Ovary of *Ranunculus*. D, The same in cross-section. E, Ovary of *Digitalis*. F, Ovary of *Campanula*.

compartment in the Umbelliferæ (Fig. 294, D). When there is but one ovule in the ovary it is generally either attached to the base (e.g. *Polygonum*) or suspended from the apex. A small number of ovules is most frequent in the more specialised families.

In certain families the loculi in the ovary become subdivided during the development of the flower. In the Cruciferæ, for instance, the bicarpellary ovary is at first unilocular, but becomes bilocular through the formation of a partition joining the two parietal placentas (Fig. 294, F). Similarly, in the Labiatæ (Fig. 432) and Boraginaceæ (Fig. 433, A) the ovary is bilocular in early stages, but subsequently exhibits four compartments. In the Flax there are ten loculi, but only five carpels.

When the ovary is apocarpous the individual carpels commonly show a spiral arrangement. In such spiral flowers a marked transition between stamens and petals is occasionally found, this being very obvious in *Nymphæa*. The same phenomenon is frequently observed in double flowers where the doubling is due to a replacement of the stamens by petals (*e.g.* cultivated Roses and Pinks).

The *ovules* of Angiosperms (Fig. 307), which in their general construction are like those of Gymnosperms, usually possess two

integuments (inner, *I.i.*, and outer, *O.i.*). A single one is the rule amongst the gamopetalous Dicotyledons (Sympetalæ) and a few polypetalous families (*e.g.* Umbelliferæ, Salicaceæ, etc.). In these latter, however, the single integument is generally relatively robust, a fact which suggests its possible origin from the fusion of two; a partial union of this character is, indeed, seen in some members of the Ranunculaceæ.[1] The *nucellus* (*n.*), with very few exceptions, is only clearly separated from the integument at the apex, where it forms a cap of tissue extending between the large megaspore (embryo sac, *e.s.*, see p. 445) and the micropyle (*m.*). The part of the nucellus in contact with the integument can often be distinguished from the latter, in sections of the ovule, by the dense contents of its cells, which form a nutritive layer around the developing embryo sac.

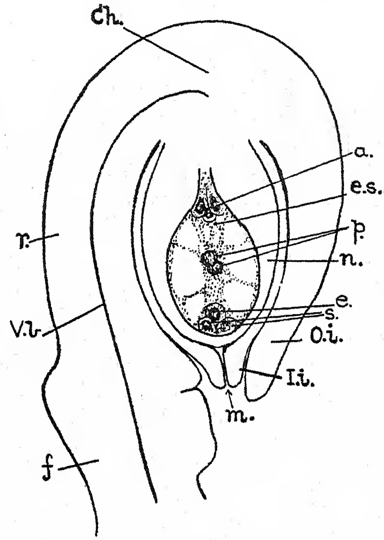

FIG. 307. Diagrammatic longitudinal section through an anatropous ovule, greatly magnified. *a.*, antipodal cells; *Ch.*, chalaza; *e.*, egg; *e.s.*, embryo sac; *f.*, funicle; *I.i.*, inner integument; *m.*, micropyle; *n.*, nucellus; *O.i.*, outer integument; *p.*, polar nuclei; *r.*, raphe: *s.*, synergidæ; *V.b.*, vascular bundle of raphe.

By far the commonest type of ovule is the *anatropous* one (Figs. 307 and 308, C), in which the main body is bent down against its stalk (*funicle*, *f.*), so that the micropyle (*m.*) is directed towards the placenta. The greater part of the funicle is connected with the adjacent portion of the outer integument, which is in consequence not easily distinguished on this side. This region, known as the *raphe* (*r.*), is traversed by the vascular bundle (*V.b.*) which enters the funicle from the placenta, and which extends as far as the base of the nucellus (a region known as the *chalaza*, *Ch.*).

Erect or *orthotropous* ovules, in which the micropyle faces away from the placenta, and lies at the opposite end to the usually short funicle (Fig. 308, B), are much less frequent, but are found, for example, in *Polygonum*. Another rare type, the *campylotropous*

[1] In a few Rosaceæ (e.g. *Geum*) there is only a single integument due to failure of the inner one to develop.

ovule (Fig. 308, E), seen in many Caryophyllaceæ, is bent in such a way that the stalk appears to be attached midway between the chalaza and micropyle. All Angiospermous ovules are supplied by a vascular bundle which runs through the funicle, but terminates at the chalaza, except in those rare instances where the nucellus is not in intimate contact with the integument. In *Myrica gale*, for

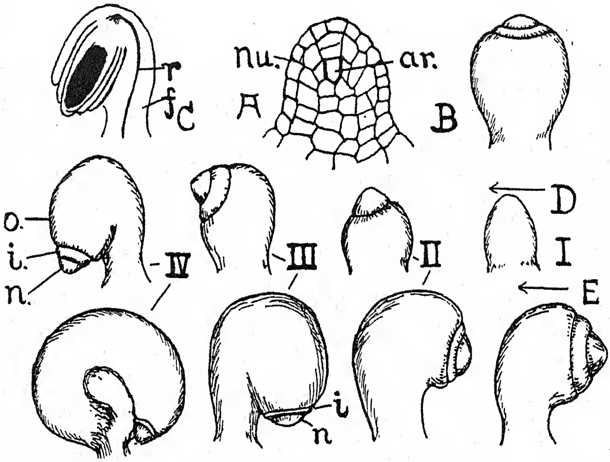

FIG. 308. Ovules and stages in their development (after Le Maout and Decaisne). A, Young ovule, before the integuments appear, showing nucellus (*Nu.*) and dividing archesporium (*ar.*). B, Orthotropous ovule of *Polygonum.* C, Anatropous ovule in longitudinal section, showing funicle (*f.*) and raphe (*r.*). D, I–IV (in the direction of the arrow), successive stages in the development of the anatropous ovule of *Chelidonium.* E, Successive stages (in the direction of the arrow) in the development of the campylotropous ovule of the Mallow (*Malva*). *i.*, inner integument; *n.*, nucellus; *o.*, outer integument.

instance, there is a well-developed vascular supply throughout the integument and the nucellus also contains conducting tissue.

The ovule invariably arises on the placenta as a small mound of thin-walled cells which represents the future nucellus (Fig. 308, A and D, I). Around the base of this the integuments subsequently develop as ring-like upgrowths, the inner being formed before the outer (II–IV). In the Spindle-tree (*Euonymus*) a third integument (*aril*) is present, which becomes conspicuous after fertilisation (Fig. 338, B, C). The caruncle of the Castor Oil seed (p. 23 and Fig. 15, A) is also of the nature of an aril.

All ovules are at first erect. The anatropous form, characteristic of the majority, is due to excessive growth on one side of the chalazal region of the rudiment, so that the latter gradually becomes curved till the micropyle points towards the placenta (cf.

Fig. 308, D). In campylotropous ovules the mature form is due to even more extreme asymmetrical growth of the chalazal region (Fig. 308, E). Stages in the development of anatropous ovules can be readily studied in transverse sections through young ovaries of the Poppy.

The first steps towards the development of a *megaspore* are to be found in very young ovules, usually before the integuments have become plainly differentiated (Fig. 308, A). As in the stamens, the *archesporium* (*ar.*) arises subepidermally, but here it usually comprises but a single cell situated near the apex of the nucellus. This divides tangentially (Fig. 308, A, *ar.*), the inner half generally constituting the mother-cell, which as a rule, by two successive divisions, of which the first is the reduction division, gives rise to a row of four spores, forming a tetrad within the nucellus. It is usually the innermost member of the tetrad that becomes the functioning megaspore (generally known as the *embryo sac*). This cell subsequently increases greatly in size so as to occupy most of the nucellus (Fig. 307, *e.s.*). In the Mistletoe-family (Loranthaceæ) no proper ovules are differentiated; a parenchymatous outgrowth, which arises from the base of the ovary and almost fills the latter, develops a number of archesporia, from each of which an embryo sac results. This affords another instance of the reduction characteristic of parasites (cf. p. 215).

Until it has reached a considerable size the embryo sac contains but a single nucleus, which usually lies in the middle of a strand of cytoplasm running from end to end of the sac and bridging a large central vacuole. Sooner or later, however, a nuclear division occurs, and the two resulting nuclei wander towards opposite ends of the embryo sac, where each again divides twice. Of the eight nuclei thus formed, three at the end remote from the micropyle, usually become separated by cell-walls and constitute the *antipodal cells* (Figs. 307, 309, 329, D, *a.*), which probably assist in the nourishment of the young embryo. They frequently enlarge after fertilisation, and may even divide to form an antipodal tissue (*e.g.* Burr-reed *Sparganium*).

Of the four nuclei at the micropylar end of the embryo sac, three become surrounded by an envelope of specialised cytoplasm, and constitute a group of naked cells known as the *egg-apparatus* (Fig. 307), which consists of the *egg* (*e.*) and two *synergidæ* (*s.*). The remaining nuclei (one at each end, one of them the sister-nucleus of the egg) pass back to the middle of the embryo sac, where these two *polar nuclei* (Figs. 307, *p.*; 329, D, *p.n.*) meet and ultimately fuse to form the *primary endosperm nucleus* (Fig. 309, *p.*). This is the stage reached by the embryo sac at the time of fertilisation.

The sequence of events during this development and the resulting structure of the embryo sac are practically identical in the vast majority of both Monocotyledons and Dicotyledons which have been investigated, and this uniformity constitutes one of the strongest arguments for the origin of the group from a common ancestry. Tubular sucker-like outgrowths from the chalazal or both ends of the embryo sac are met with in the Beech, Hornbeam, and some Sympetalæ (*Plantago lanceolata*, Scrophulariaceæ), and probably aid in the transference of food-material to the developing embryo. The same end is served by the haustorial outgrowths from the later-arising endosperm (p. 469) which occur in some genera.

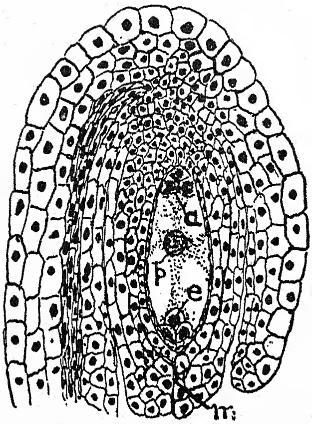

FIG. 309. Longitudinal section of ovule of Marsh Marigold (*Caltha*), showing the structure of the mature embryo sac. *a.*, antipodal cells; *e.*, egg; *m.*, micropyle; *p.*, primary endosperm nucleus.

The pollen grains and embryo sacs of Angiosperms are obviously comparable to the microspores and megaspores of Gymnosperms and *Selaginella*, and within them divisions take place which lead to the formation of the male and female gametes respectively. The contents of the embryo sac may therefore be regarded as a female prothallus, and the contents of the microspore (cf. p. 468) as a still more reduced male prothallus.

CHAPTER XXXVI

FLORAL MECHANISMS AND POLLINATION [1]

THE ovules do not, except in rare cases, mature into seeds, unless pollen from the same kind of plant has been deposited upon the stigma at a time when the latter is still in a receptive condition. By carefully removing the stamens from a number of flowers, before their pollen is shed (*i.e.* in the bud-stage), and then covering each with a bag of fine muslin to prevent access of insects or of wind-borne pollen, the necessity of pollen for the formation of seed can be readily shown. If pollen from another plant of the same kind is transferred to the stigma of one of the flowers, with the help of a camel's-hair brush, ripe seed will, however, almost certainly be produced.

Experiments have also proved that in many plants a larger number of seeds and frequently more vigorous offspring are produced, if fertilisation is effected by pollen from the flower of a different individual of the same species. This is called *cross-pollination*, whereas the term *self-pollination* is applied when the pollen comes either from another flower of the same individual or from the stamens of the self-same flower, the former alternative being sometimes more beneficial than the latter. The advantage of cross- as compared with self-pollination is very apparent in some plants; for instance, Darwin found that the weight of Cabbages produced from seeds, formed as a result of cross-pollination, was very much greater than those grown from seeds which had been produced by self-pollination, the former varying between 74 and 130 ounces, the latter between $11\frac{1}{2}$ and 46 ounces.

In view of such facts it is not astonishing that a very large number of flowers exhibit a structure which tends to favour cross-pollination. Most flowers contain both stamens and ovaries—in other words, are *hermaphrodite* (indicated by the symbol ☿), but the two kinds of organs rarely ripen at exactly the same time. The stamens may ripen first (*protandrous* flowers), or the stigma matures before the pollen is shed (*protogynous* flowers). There

[1] For reference-books, see p. 466.

are, however, all transitions from flowers in which the essential organs ripen almost simultaneously (*e.g.* White Dead-nettle) to flowers in which the one kind of organ has withered before the

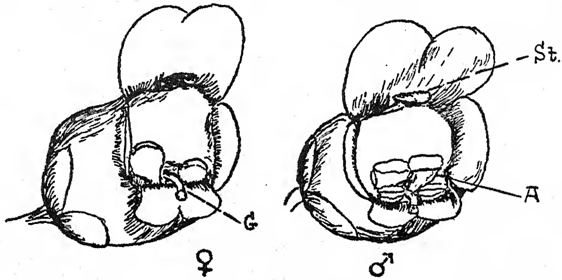

FIG. 310. Flowers of the Figwort (*Scrophularia*), to illustrate protogyny (enlarged). The left-hand flower is in the female stage, whilst in the right-hand one the stigma has withered and the stamens are mature. A, stamen; G, stigma; *St.*, staminode.

other is mature. Thus, extremely protandrous flowers are seen in the Canterbury Bell and Rose-bay Willow-herb (Fig. 311), whilst marked protogyny is exhibited by the Figwort (Fig. 310) and Plantain (Fig. 313).

The tetramerous flower of the Willow-herb has eight stamens and a four-lobed stigma, but until the stamens have finished

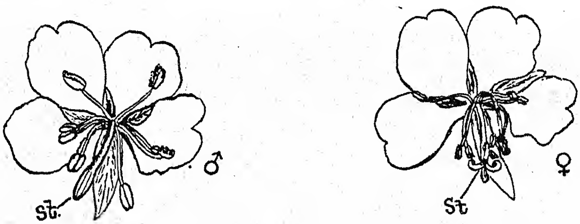

FIG. 311. Flowers of Rose-bay Willow-herb (*Epilobium angustifolium*), to illustrate protandry (natural size). In the left-hand flower the stamens are alone mature; in the right-hand one they have withered, whilst the four stigmatic lobes are now spread out. *St.*, stigma. ♂, male stage; ♀, female stage.

shedding their pollen (*i.e.* until the male or staminate stage is over) the stigmatic lobes remain closely pressed together, so that their receptive surfaces are not exposed (Fig. 311, ♂). When the stamens wither, the four lobes of the stigma curl back (Fig. 311, ♀, *i.e.* the flowers are now in the female or pistillate stage), ready to receive pollen from some flower which has opened later. In the spike of the Plantain (Fig. 313) the lower flowers open first

and exhibit a white feathery protruding stigma, but at this stage no stamens are to be seen; as the flowers in the upper part of the inflorescence develop, the stigmas of the lower ones wither and their place is taken in each flower by the four stamens. Since the flowers in the female stage (Fig. 313, ♀) are always above those in the male (Fig. 313, ♂), the pollen in falling cannot effect pollination.

In all such extreme instances, self-pollination is obviously prevented in the earlier stages of flowering, although a considerable number of such flowers may become self-pollinated just before fading (p. 465). If, however, prior to this, cross-pollination has taken place, pollen from the same flower is ineffective. In fact, in many Leguminosæ, for instance, such pollen often has no effect at all.

Of the commonly cultivated fruits, most of the bush-fruits and small fruit (*e.g.* Currants, Gooseberries, Raspberries, Blackberries, Strawberries, etc.) are self-fertile. This is also true of Medlar, Quince, Apricot, Almond, and Peach, but many varieties—though not all—of Apple, Pear, Plum, and Cherry are more or less self-incompatible—that is to say, self-pollination cannot normally be effected, very commonly owing to a marked retardation in the growth-rate of the pollen tube. Hence the desirability of growing several varieties together. Even in the case of self-compatible varieties better crops usually result from cross-pollination.

Greater certainty of cross-pollination is ensured, when stamens and ovaries occur in distinct *unisexual* flowers. The two sexes are either found on the same individual (*monœcious*, e.g. Hazel, Fig. 314), or on different individuals (*diœcious*, e.g. Dog's Mercury, Fig. 295; Willow, Fig. 418). In the latter self-pollination is out of the question. Not uncommonly such unisexual flowers show remains of the other essential organ and so betray their derivation from an hermaphrodite condition. Thus, in the staminate flowers of the Buckthorn (*Rhamnus*) a rudimentary ovary surmounted by a style can be recognised at the base of the perianth-tube. We could regard such male flowers as extremely protandrous ones in which the female stage is never attained, and a similar explanation could be applied to pistillate flowers.

Quite a large number of plants possess unisexual flowers side by side with hermaphrodite ones. Thus, in many Compositæ the outermost flowers (*ray-florets*), with a strap-shaped (ligulate) corolla, are female (Fig. 299, F; Fig. 312, B), whilst those occupying the greater part of the capitulum (*disc-florets*) and having tubular corollas are hermaphrodite and protandrous (Fig. 297, E; Fig. 312, C). In the Coltsfoot (*Tussilago*), however, the disc-florets are

male, having but a rudimentary ovary, whilst the ray-florets are, as before, female. It may be added that in certain groups of Flowering Plants all sorts of variations in the distribution of sexes are to be found. In *Lychnis*, for instance, male, female, and hermaphrodite flowers occur on distinct plants, whilst in the Ash (*Fraxinus*) all three types may be borne on the same individual.

Minor features that tend to favour cross-pollination are the extrorse dehiscence of stamens (p. 440) and arrangement of the

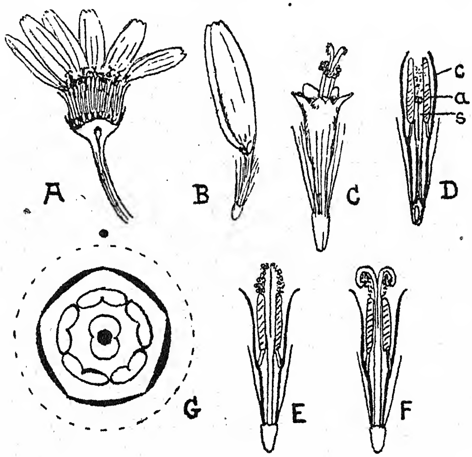

FIG. 312. Floral structure and pollination in *Senecio aquaticus* (A, natural size, other figures somewhat enlarged). A, Capitulum in longitudinal section. B, Ray-floret. C, Disc-floret in early female stage. D, Ditto, in longitudinal section, in early male stage. E, Ditto, with style just emerging. F, Ditto, late stage. G, Floral diagram of disc-floret. *a*, stamen; *c*, corolla; *s*, style.

anthers at a lower level than the stigma in many upright flowers or *vice versa* in hanging ones.

Pollination can be effected by various agencies, the commonest being insects and wind, more rarely water (p. 554). Wind-pollination (*anemophily*) is a mode of transference associated frequently with simple types of flowers, particularly unisexual ones. It is evident that this mode of pollination depends largely on chance and therefore, if it is to be successful, a much greater amount of pollen must be produced than is necessary to effect fertilisation. Wind-pollinated plants either have numerous stamens in their flowers (*e.g.* Poplar, Elm), or relatively large anthers producing copious pollen (*e.g.* Grasses, Fig. 439, A) or the male flowers are numerically in excess of the female (*e.g.* Hazel). Moreover, the stigma is frequently branched and feathery (*e.g.* Grasses, Fig. 439, A; Hazel, Fig. 314, ♀), so that pollen is the more easily caught.

The ready liberation of the pollen of anemophilous flowers is facilitated by the frequent occurrence of loose hanging inflorescences (*e.g.* Birch), or of anthers which are loosely hinged on long projecting filaments, so that they are moved by the least breath of wind (Grasses, Figs. 301, D, and 439, A; Plantain, Fig. 313). The dry and powdery pollen grains do not adhere to one another, thus facilitating a wider distribution.

The flowers of wind-pollinated plants are usually inconspicuous and green, either possessing a simple perianth (*e.g.* Dog's Mercury, Fig. 295) or are naked (*e.g.* Ash). They naturally lack all those attractive mechanisms which are so marked a feature of the insect-pollinated flower.

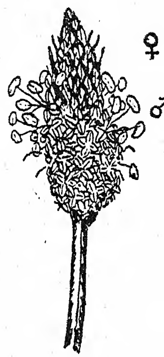

FIG. 313. Spike of the Black Plantain or Ribwort (*Plantago*) (natural size). The upper flowers, which have opened most recently, are in the female (♀) stage, whilst the middle ones are in the male (♂) stage, and the lowest of all are already fading (cf. p. 448).

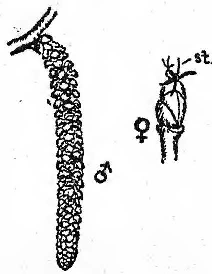

FIG. 314. Male (♂) and female (♀) catkins of the Hazel (*Corylus*) (natural size). *st.*, stigmas.

Entomophilous flowers are visited by insects either for their nectar or pollen and are usually very conspicuous. Nectar is the most frequent attraction and is produced in *nectaries* (p. 198) which may be situated on almost any protected part of the flower. Dark lines, known as *nectar-guides* (*e.g.* Pansy, Fig. 325, A), are sometimes found upon the petals converging towards their base where the nectar is formed. Experiments have shown that such markings probably aid the more intelligent insects in finding the nectar rapidly.

Nectaries are frequently located at the base of the flower and most often on an enlargement of the thalamus known as a *disc* (*e.g.* the Rue, Fig. 315, B, *n*) which may be confined to the anterior side of the ovary (as in many Labiatæ and Scrophulariaceæ). In flowers with an inferior ovary (p. 430) the disc is situated on the top of the latter (*e.g.* Umbelliferæ, Fig. 315, E, *n*). Many members

of the Liliaceæ (*e.g.* Tulip) develop nectaries in the wall of the ovary itself, these appearing as narrow slits when the latter is cut across. In other flowers the nectaries are produced on the expanded bases of the stamens (Fig. 315, C, *n*, and other Caryophyllaceæ).

In different members of the Ranunculaceæ all conditions are found between petals with a nectary at the base, protected by a small flap (Buttercup, Fig. 315, A), and little trumpet-shaped

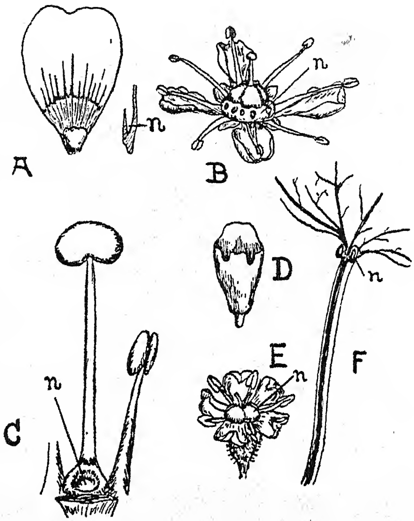

FIG. 315. Forms of nectaries (A, B and F, natural size; other figures enlarged). A, Petal of Buttercup, showing flap covering nectary; the right-hand figure the same in longitudinal section. B, Flower of Rue (*Ruta*). C, Stamens of *Stellaria*. D, Honey-petal of *Helleborus*. E, Flower of Hogweed (*Heracleum*). F, Part of leaf of *Viburnum opulus*, showing extrafloral nectaries. *n*, nectaries.

structures (as in the Christmas Rose, Fig. 315, D; and Winter Aconite, Fig. 296) situated just outside the stamens.

Nectaries often produce such large quantities of nectar that it overflows from the depressions in which it is secreted and may in some flowers accumulate in special *spurs*. These are but slightly developed in the Cruciferæ (Fig. 317, *b*) where they are formed by the pouch-like bases of the lateral sepals situated opposite the two short stamens bearing nectaries (cf. Fig. 424, A). In the Toadflax and Garden Nasturtium (Fig. 297, A) they appear as tube-like outgrowths of the perianth. The spur may, however, not merely function as a receptacle for nectar, but may actually produce it at its tip; this is seen in Orchids (Fig. 326, B, *sp.*) and in *Aquilegia*, each petal of the latter being prolonged into a spur. In such

flowers a special outgrowth has developed for the purpose of producing nectar, and a similar feature can be observed in the Pansy (Fig. 325, A and B, *n*) and Larkspur in which two processes, from the stamens and petals respectively, project into the spur and secrete nectar into it.

Not all entomophilous flowers, however, produce nectar, a limited number providing no other bait than pollen. Such *pollen-flowers* (e.g. *Hypericum, Papaver*) usually possess a large number of stamens, so that there is an adequate surplus of pollen for pollination. It may be added that, even in flowers having nectaries, insects generally take a certain amount of the pollen as food.

Many flowers are so constructed that nectaries and pollen are protected from the injurious effects of dew or rain. The simplest method of pollen-protection is for the dehisced anther to close up more or less completely (cf. p. 440). The closing of flowers or capitula at night (p. 268) serves to shield both nectar and pollen, and the same end is attained by the hanging position occupied by many flowers (e.g. *Campanula*, Fig. 299, A). The individual flowers in many catkins (*e.g.* Hazel, Fig. 314, ♂) are protected by the bracts which appear as roofs above them.

While nectar and pollen are the attraction, the colours, odours, and grouping of flowers render them conspicuous. As a general rule the perianth provides the *attractive apparatus*,[1] but sometimes stamens (*e.g.* Willows, *Thalictrum*) or even bracteoles (*e.g.* some cultivated Sages, *Bougainvillea*) may play a part. A great feature in plants possessing small flowers is the massing together of the latter, whereby a conspicuous inflorescence is formed (cf. p. 428). Moreover, where the inflorescence is flat-topped, the outermost flowers are often irregular and exhibit a one-sided enlargement of the corolla tending to produce greater conspicuity, a feature which is well illustrated by the Candytuft (Fig. 316), Hogweed, Daisy, etc.; not uncommonly these outer flowers are unisexual (many Compositæ, p. 449 and Fig. 312, B) or altogether devoid of essential organs (*i.e.* are *neuter*, as in the Guelder-rose (*Viburnum opulus*) and *Centaurea*, Fig. 435, B), so that they are purely attractive in function.

Since, provided they are visited, pollination is almost a certainty in entomophilous flowers, particularly those frequented by Bees, a much greater economy in pollen can be effected than in anemophilous plants. There is usually (except in pollen-flowers) a relatively small number of stamens, a feature which becomes the more marked the

[1] The importance of the perianth in this respect may be shown by removing all the petals from one specimen of a certain plant, out of doors, and noting the behaviour of insects in relation to it, as compared with a normal plant.

more perfect the mechanism for pollination. The rough or sticky coat of the pollen causes it to adhere readily to the insect's body, whilst the stigma has a sticky receptive surface and is not as richly branched as in most wind-pollinated types.

The chief pollinating insects are Bees, Butterflies, Moths, Flies, and Beetles. The Honey Bee and other Hymenoptera are most important, but Diptera play a large part in the pollination of some flowers (*e.g.* Blackberry). All pollinating insects, except Beetles, possess a special sucking organ, the *proboscis*, arising from the under side of the head, very short in Flies and exceptionally long in Butterflies and Moths, where it is coiled up when not in use. When visiting a flower the position taken up by an insect depends largely on the length of its proboscis and the situation of the nectary. In fact, flowers possessing a long narrow corolla-tube (Fig. 293, B) or a spur are not accessible for nectar to any but long-tongued insects, whilst wide open flowers (Fig. 293, A) provide nectar for a variety of visitors, both with long and short proboscides. Certain insects (*e.g.* the small Bumble-bee), however, not uncommonly puncture the base of the corolla-tube, when this is too long for them to reach the nectary by legitimate means, and thus steal nectar without effecting pollination.

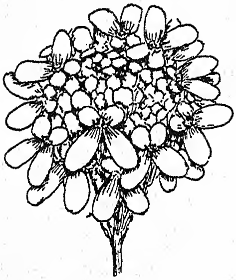

FIG. 316. Inflorescence of the Candytuft (*Iberis*) (natural size), showing the enlarged marginal flowers.

In the majority of flowers the insects concerned actually alight on the perianth, although many Moths hover in front of the flowers they visit. As a result of the different, though for the same flower usually constant, positions taken up by pollinating insects very diverse parts of the body (viz. proboscis, head, back, or abdomen) may become dusted with pollen, and these are often covered with hairs to which the pollen readily adheres. Sooner or later the stamens and stigma in any given entomophilous flower come to occupy similar positions, so that the pollen taken from the anthers of one flower will be likely to get rubbed against the stigma of another.

The simplest kinds of *pollination-mechanisms* are seen in regular flowers, amongst which two principal types can be distinguished. The first are flowers with an open shallow corolla (*e.g.* Buttercup, Fig. 293, A), and from these almost any insect-visitor can obtain nectar. The insect here alights either on the corolla or on the

essential organs, so that either its head or its under side becomes dusted with pollen. Flowers of this type are often visited by small insects which may in their erratic wanderings effect pollination, although no doubt it is often only pollen from the same flower that is transferred. Insects commonly crawl about on the flat tops of umbels, corymbs, and capitula, and, since many of the plants concerned are markedly protandrous, pollen is transferred from the younger flowers in the centre to the older ones near the margin.

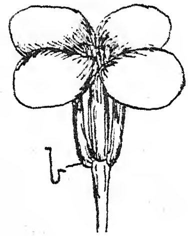

FIG. 317. Flower of the Wallflower (*Cheiranthus*), showing the tube produced by the four upright sepals and the claws of the petals (natural size). *b*, one of the pouched sepals.

The second type of regular flower, the *tubular* one, possesses a perianth-tube of varying length and formed in one of two ways. Most usually, as in the Primrose (Fig. 318) and *Narcissus* (Fig. 293, B), the corolla or perianth is gamopetalous, the united portions producing the tube. But where the petals of a polypetalous corolla have long claws (Fig. 298, A) they, together with the upright sepals, constitute a tube (*e.g.* Cruciferæ, Fig. 317). In all such flowers the expanded ends of the petals form an alighting platform (Fig. 293, B) and the pollen is brushed off either on to the proboscis or the head of the insect, according to the level at which the anthers stand in the tube. Such flowers are only visited with profit by long-tongued insects, the variety of visitors becoming the more restricted the greater the length of the tube.

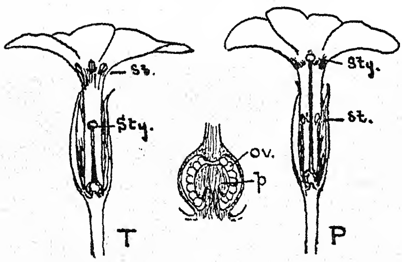

FIG. 318. Floral structure of *Primula*, showing longitudinal sections of thrum-eyed (T) and pin-eyed (P) forms (natural size). *St.*, stamens; *Sty.*, stigma. The middle figure shows the ovary in longitudinal section, considerably enlarged. *ov.*, ovule; *p*, free central placenta.

A special device, spoken of as *heterostyly* and tending to favour cross-pollination, is seen in certain tubular flowers (*e.g.* Primrose, Fig. 318) in which more than one type of flower is produced. Some individuals have the stigma situated at the mouth of the corolla-tube (pin-eyed form), the stamens occupying a position half-way down (Fig. 318, P), whilst in others the relative positions of stamens and stigma are reversed (thrum-eyed form, Fig. 318, T). As a consequence the pollen received upon the proboscis from a flower

of the pin-eyed type will only be at the appropriate level for effecting pollination in one of the thrum-eyed type, and *vice versa*.

More perfect pollination-mechanisms are found in flowers having an irregular corolla, which results in a greater restriction of insect-visitors. In such flowers the agent is compelled to take up a definite position with reference to the essential organs and must frequently be strong enough to force open the more or less closed corolla.

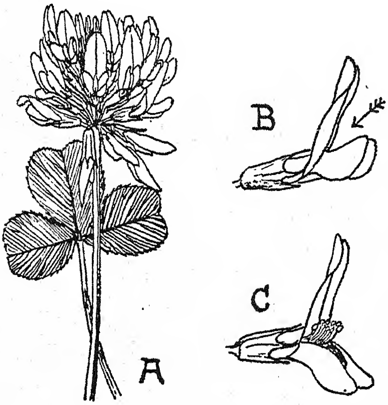

FIG. 319. Pollination in the Clover (*Trifolium*) (A, natural size; B and C enlarged). A, Inflorescence and leaf. B, Single flower seen from the side, in its normal condition. The arrow indicates the direction of approach of the pollinating insect. C, The same, showing position of parts at time of pollination when wings and keel are depressed.

As a first example the flowers of British Leguminosæ may be studied. Here the corolla (Fig. 320, A; cf. also Fig. 294, C) consists of: (i) a large posterior petal, the standard, usually vertical (Fig. 320, A and C, *s*); (ii) a pair of wings (*w*) situated at the sides; and (iii) a pair of anterior petals, more or less joined together to form the boat-shaped keel (*k*). The essential organs are completely enclosed within the keel (see Fig. 321, E) and are thus efficiently protected; they consist of ten stamens (cf. Fig. 294, C), often of two lengths, the filaments forming a tube around the central pod-like ovary which is provided with a long style ending in a stigma (Fig. 321, D, *St.*). Nectar is usually produced on the inner sides of the bases of the filaments and accumulates in the trough formed by them. In such nectar-producing flowers the posterior stamen is always free (cf. Fig. 294, C), thus leaving a slit in the stamen-tube through which the proboscis is inserted. Some Leguminosæ (*e.g.* the Broom, Lupine), however, produce no nectar, and in these pollen-flowers all the ten stamens are united (cf. Fig. 426, A).

The wings form the alighting platform, the head of the insect being directed towards the conspicuous standard (cf. Fig. 319, B). Since obviously neither nectar nor pollen are easily reached, these flowers can only be visited with profit by sufficiently intelligent insects and by such as are heavy enough to expose the essential organs; Bees fulfil both requirements and are indeed amongst the commonest visitors. The base of each wing is provided with an

outgrowth which fits into a hollow in the adjacent petal of the keel (Fig. 320, D) and thus, when a Bee alights on the wings, these and the keel are depressed simultaneously. As a result the essential organs are exposed and rub against the *under surface* of the insect's body (cf. Fig. 319, C). Although the stigma is often surrounded

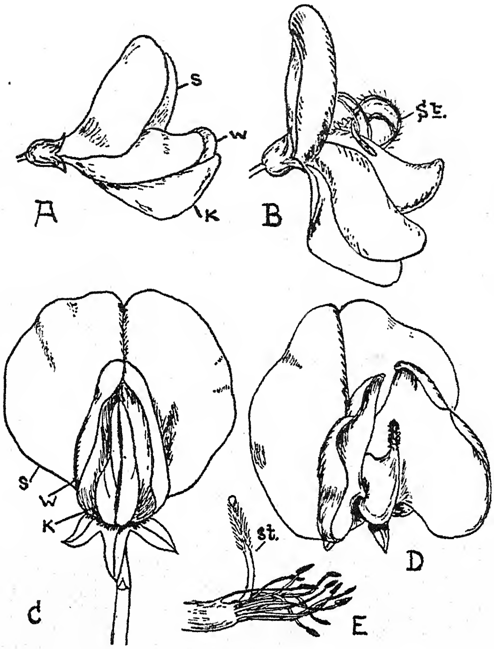

FIG. 320. Pollination in the Broom (*Cytisus scoparius*) and Sweet-pea (*Lathyrus odoratus*) (natural size, E enlarged). A, Flower of Broom before pollination, seen from the side. B, Ditto after pollination. C, Flower of Sweet-pea, seen from the anterior side. D, Ditto, with stigma and stylar brush emerging, as during pollination. E, Essential organs enlarged, showing position when released from keel. *k*, keel; *s*, standard; *St.*, style; *w*, wings.

by pollen, as it lies hidden in the keel, self-pollination does not occur owing to self-incompatibility (p. 449). When the insect flies away, the parts of the flower return to their original positions and the keel again screens the essential organs. This simple type of pollination-mechanism is seen in the Clover, Sainfoin, and Melilot.

In the Sweet-pea and Vetches the style, just beneath the small stigma, bears a dense brush of hairs (Fig. 320, E, *st.*) upon which the pollen is shed. The tip of the keel in the Sweet-pea is prolonged into an upright beak (Fig. 320, D) in which are situated

the anthers of the ten stamens, surrounding the stigma and stylar brush. When a Bee alights on the wings and the keel is depressed, the style emerges (Fig. 320, D) brushing out the pollen onto the insect's under surface, whilst the stamens remain concealed; the relative positions of style and stamens are now approximately as in Fig. 320, E.

In the Lupine and Bird's-foot Trefoil (Fig. 321) the two petals

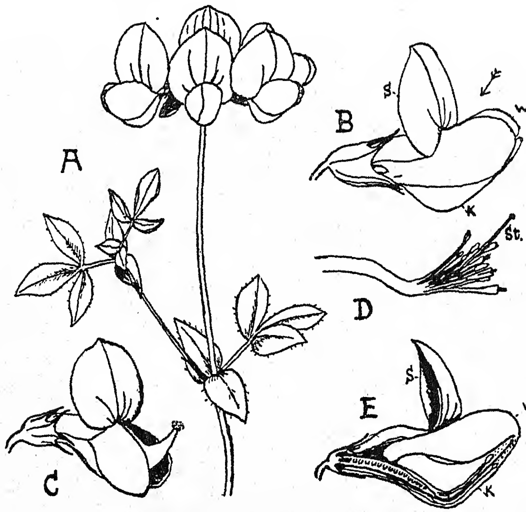

FIG. 321. Pollination in the Bird's-foot Trefoil (*Lotus corniculatus*) (A, natural size; B–E enlarged). A, Portion of plant with inflorescence. B, Side-view of flower before pollination; arrow marks direction of approach of insect. C, Flower during pollination, showing emergence of pollen. D, Essential organs. E, Longitudinal section of flower. *k*, keel; *s*, standard; *St.*, style; *w*, wings.

of the keel are joined along both their lower and upper edges, leaving, however, a small circular opening near the pointed tip (Fig. 321, C and E). The tops of the filaments of the five longer stamens are swollen (Fig. 321, D), so as to form collectively a piston by means of which the pollen collecting in the tip of the keel is forced out of the opening, when the keel is depressed (Fig. 321, C). The style is appreciably longer than the stamens, so that the stigma is the first to protrude, when an insect alights on the flower. In all these flowers the different parts return to their normal positions when the visitor flies away.

In the *explosive flowers* of the Broom (Fig. 320, A and B) and Gorse, however, the style and stamen-tube are compressed into a relatively small keel so that, when an insect of sufficient weight alights on the wings, the depression of the keel leads to a sudden release

of the essential organs; the latter emerge with a jerk and a shower of pollen is sent over the visitor. No return of the floral organs to their previous positions takes place; the flower is "exploded" and stamens and stigma remain projecting from it (Fig. 320, B).

The pollination of the Broom is so far exceptional in that some of the pollen is deposited *on the back* of the insect. When the latter alights, the five shorter stamens first emerge and strike its under surface, but immediately afterwards the five longer stamens and the stigma spring out (Fig. 320, B) and strike the insect's back. The pollen received by the lower side of the body probably serves as food.

In the Labiatæ and in many Scrophulariaceæ all the pollen is deposited *on the back* of the insect. The usually horizontal flowers of most Labiatæ exhibit a corolla-tube (Fig. 299, D), the upper part of which is drawn out into a helmet-shaped hood (*h*), formed by the two posterior petals and constituting a roof over the four stamens and the bilobed stigma. The anterior part of the corolla forms an alighting platform (*p*), whilst projections (*l*) on either side of the throat give a hold to the fore-feet of the insect during pollination. Nectar is secreted by a disc (p. 451) at the base of the ovary but, owing to the presence of a corolla-tube, can only be reached by long-tongued insects, such as will have a body sufficiently large to fill the space between the upper and lower lips. Frequently hairs are present in the upper part of the tube, which tend to prevent the intrusion of small insects which would steal nectar without effecting pollination. In probing the nectary the visitor brings its back into contact with the essential organs and thus effects pollination. The flowers are commonly protandrous, the stamens first projecting downwards to a slight extent so that they are bound to touch legitimate visitors, the stigma at this stage being above them and with its two lobes pressed together; subsequently the latter diverge and the stigma comes to lie a little below the position previously held by the stamens.

A more specialised condition is seen in *Salvia* (Fig. 322) whose flowers have only two stamens, each with a much elongated connective joining the two anther-lobes (cf. p. 435 and Fig. 322, E, *co.*). One arm of the connective is somewhat longer than the other, and the anther-lobe at the end of the short arm produces no pollen. These sterile lobes are so placed in the throat of the corolla-tube that an insect probing for nectar must push against them (Fig. 322, A and D), thus bringing the fertile lobes down upon its back (Fig. 322, B). In the female stage the stigma projects to a very marked extent (see Fig. 322, C), so that its lobes are bound to touch the back of an insect-visitor.

Amongst the Scrophulariaceæ we have flowers with a pollination-mechanism very similar to that of Labiatæ (*e.g.* Red Eyebright, *Bartsia*, Fig. 372, A). The same type of construction is seen also in the flowers of the Musk, the sensitive stigma of which (cf. p. 266) is a special device that prevents self-pollination. The folding together of the two lobes (Fig. 171, B) is brought about by contact with the pollen-bearing proboscis of an insect, self-pollination being thus prevented. In *Antirrhinum* (Fig. 323) and Toadflax (*Linaria*) the mouth of the corolla is completely closed by a pouch-like outgrowth from the lower lip (Fig. 323, A and C, *p*). In this way pollen and

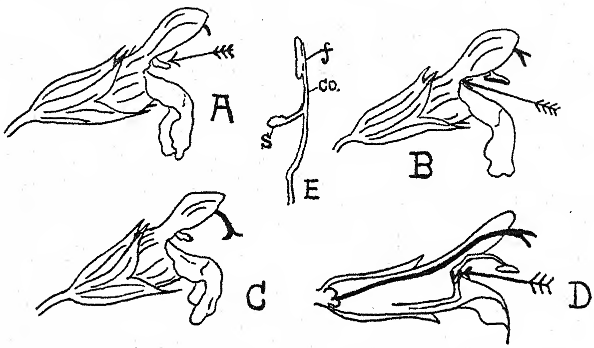

FIG. 322. Pollination in *Salvia* (all figures natural size). A, Flower before pollination, in male stage. B, Flower during pollination. C, Female stage. D, Flower in longitudinal section, showing mode of pollination. E, Single stamen (slightly enlarged). The arrows show direction of approach of pollinating insect. *co.*, connective; *f*, fertile lobe; *s*, sterile lobe of stamen.

nectar are not only amply protected from outside moisture, but the flower is alone accessible to insects (*e.g.* Bumble-bees) which are strong enough to force open the flower. In the Figwort (Fig. 310) the stigma (♀) and stamens (♂) successively occupy positions against the lower lip, so that the under side of the insect (often a Wasp) is effective in pollination.

Further examples of special pollination-mechanisms are furnished by the Monkshood, Pansy, and Orchids. In the first, each flower has a petaloid perianth composed of a large posterior hood (Fig. 324, *h*), overlapping the four lower segments (*l*, *a*). Within the hood are situated two long-stalked nectaries (Fig. 324, B, *n*), numerous stamens (*s*), and an apocarpous ovary (*o*). The insects (Bumble-bees) alight on the lateral and anterior members of the perianth and probe for nectar beneath the hood, so that their under side becomes dusted with pollen in the first (male) stage of the protandrous flower. Subsequently the stamens curl

right back, so that in the female stage the stigmas touch the Bee's abdomen.

In the Pansy (Fig. 325) the anterior petal (*a*) serves as the landing-place for the insect, which then pushes its proboscis (the arrow in Fig. 325, A) into the spur (*sp.*, cf. p. 453) containing the nectaries borne by the two anterior stamens (Fig. 325, B, C). The five stamens fit closely around the style. The receptive portion of the stigma (Fig. 325, D) is a small hollow on its anterior face (*st.*) covered by a flap (*fl.*) hinged towards the base of the flower. The pollen is shed on the proboscis, and, in its withdrawal, the flap over the stigmatic surface is closed, so that self-pollination in these flowers is impossible (cf. p. 465). When visiting another flower the proboscis pushes back the flap and the pollen is thus deposited on the stigmatic surface. The Violets have quite similar flowers, but the style is differently shaped and the flap is often lacking.

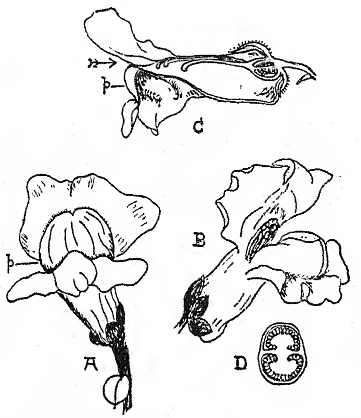

FIG. 323. Pollination in *Antirrhinum* (D enlarged, other figures about two-thirds natural size). A, Complete flower seen from the anterior side. B, Flower in side-view, with the corolla forced open to display the essential organs beneath the upper lip. C, Flower in longitudinal section. The arrow marks the direction of approach of the insect. D, Cross-section of ovary, showing the large axile placenta. *p*, pouch formed by lower lip of corolla.

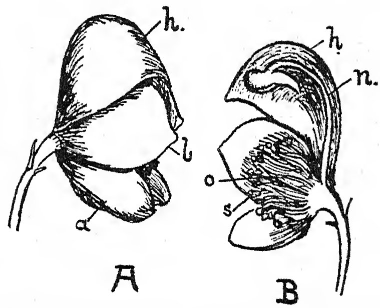

FIG. 324. Flowers of the Monkshood (*Aconitum*) (natural size). A, Entire flower seen from the side. B, Flower in longitudinal section. *a*, anterior member; *h*, hood (posterior member); *l*, lateral member; *n*, nectary; *o*, ovary; *s*, stamens.

Many British Orchids show a very complex mechanism. In the Early Purple Orchis (Fig. 326) the irregular perianth consists of two whorls, each of three members (cf. Fig. 326, C), the posterior petal (*labellum*) of the inner series forming an alighting platform (*l*) and being drawn out into a long spur (*sp.*). Owing to the twisting of the sessile flower through half a circle, in the course of its

development, the labellum occupies an anterior position, the twisting of the inferior ovary (*o*), which is elongated and resembles a flower-stalk, being very apparent. The remaining five petals form a protective hood over the essential organs (Fig. 326, A and B). The latter (Fig. 326, D) occupy the centre of the flower and are situated on a short column (*c*), the upper part of which bears a single large stamen with two very distinct anther-lobes. Each lobe contains a mass of pollen grains (*pollinium*, p. 438) cohering by sticky threads which are continued below into short stalks (*ca.*); the latter end in little sticky swollen discs contained in a shallow pouch (*r*) which forms a slight projection on the column, somewhat overhanging the mouth of the spur. Below this pouch, and on either side of it, are seen the two broad flat stigmatic surfaces (*s*) which are more or less joined together. Above them two small teeth, representing barren stamens or staminodes (*Std.*), are distinguishable.

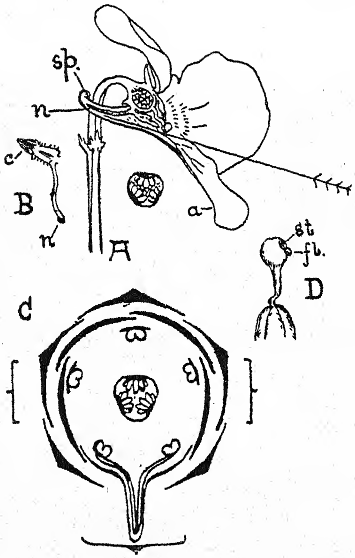

FIG. 325. A–C, Structure of flower of Pansy (*Viola tricolor*). A, Longitudinal section of flower (natural size). B, Single stamen (enlarged). C, Floral diagram. D, Ovary, etc., of *V. arvensis* (enlarged). *a*, alighting platform; *c*, connective of anther; *fl.*, flap below stigmatic surface; *n*, nectary; *sp.*, spur; *st.*, stigma.

An insect settling on the labellum has to pierce the tissue at the base of the spur for nectar and, whilst thus occupied, its head necessarily comes into contact with the pouch (*r*). As a result the pollinia adhere to it and, when the visitor flies away, it carries them projecting vertically from its head. In the space of half a minute their stalks bend forwards through a right angle. When a new flower is visited, the pollinia are therefore in the correct position to strike against the stigmas.

The Compositæ exhibit a pollination-mechanism quite different from those hitherto considered, and as a general rule the hermaphrodite florets alone produce seed. Pollen is shed into the tube formed by the five joined anthers (Fig. 312, D). At this stage the two receptive surfaces of the stigma are in contact, the style being

quite short. When the stamens have dehisced the style grows so that the numerous hairs on its upper part gradually brush the pollen out of the top of the anther-tube (Fig. 312, E). By continued growth the stigma is carried beyond the anthers and soon after its two lobes diverge (Fig. 312, C), thus exposing the receptive surfaces above the mass of pollen.

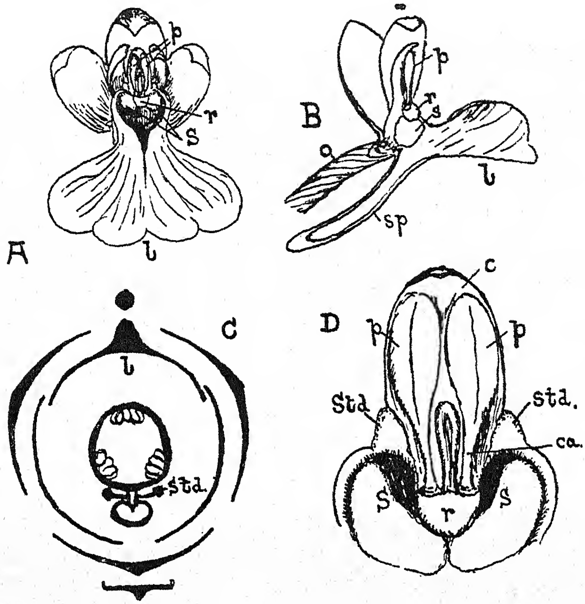

FIG. 326. Structure of flower of Early Purple Orchis (*Orchis mascula*) (A and B somewhat enlarged, D considerably magnified). A, Entire flower, seen from the front. B, Flower in longitudinal section, except for ovary which is shown entire. C, Floral diagram. D, Column with essential organs. *c*, column; *ca.*, stalk of pollinium; *l*, labellum; *o*, ovary; *p*, pollinium; *r*, pouch; *s*, stigma; *sp.*, spur; *Std.*, staminode.

The nectar is produced around the base of the style. Owing to the relatively short corolla-tube the capitula are visited by a variety of insects, chiefly Bees and Flies. These become dusted with pollen on their under surface and, as often as not, merely transfer it from one floret of the capitulum to another. As the flower gets older the lobes of the stigma continue to diverge till they curl right back, as in Fig. 312, F, thus bringing their receptive surfaces into contact with the pollen still adhering to the hairs on the style. In this way self-pollination is assured, if cross-pollination has not already taken place (cf. p. 465).

The different kinds of Bees are by far the commonest insect-

visitors to the irregular flowers considered above, and this applies especially to those which are blue, a colour for which Bees seem to have a decided preference. Owing to the fact that many Bees visit only one kind of flower at a time, they are the most useful agents in pollination. Butterflies, on the other hand, seem to be attracted chiefly by white and red flowers and, where these have a relatively long corolla-tube, these insects may be the most important visitors (*Lychnis*, *Silene*). A considerable number of flowers have become markedly adapted to pollination by night-flying Moths (*e.g.* Evening Primrose, Tobacco, Honeysuckle, Fig. 327, White Jasmine), inasmuch as many only open at night and at this time alone emit a strong scent. Such flowers are mostly white or yellow so that they are relatively conspicuous in the dusk and, since Moths usually hover in front of the flower (p. 454), no alighting platform is necessary and the flowers are frequently regular.

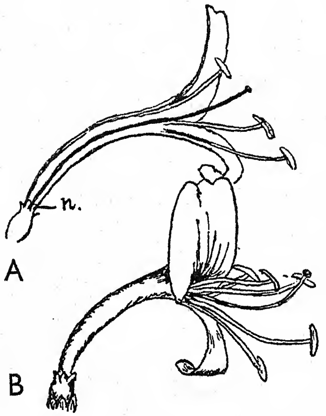

FIG. 327. Structure of flowers of Honeysuckle (*Lonicera*) (natural size). A, In longitudinal section. B, Entire flower in side-view. *n*, nectary.

Flowers visited chiefly by flies are often characterised by a fœtid odour and a dirty brown or purplish colour, as in Herb Paris (*Paris quadrifolia*) and Cuckoo-pint. Pollination in the latter (Fig. 328) results from imprisonment of the insects concerned. The fleshy spike bears the naked unisexual flowers on its lower portion only, those at the very base being female (each consisting of one carpel) and those above male (each with 2 to 4 stamens); beyond these are a number of downwardly curved hairs (*h*) which wither about the time that the stamens shed their pollen. The upper half of the spike is dilated to form a purple club-shaped structure. The whole inflorescence is enveloped in a large sheathing bract, the lower part of which forms a tube narrowing to a waist, at the level where the hairs above mentioned are situated, whilst the upper portion expands into an open leafy structure exposing the swollen tip of the axis (Fig. 328, A). Small Flies (Midges), attracted by the latter and the evil odour, crawl down into the swollen base of the tube; their escape is temporarily prevented by a slippery, oily surface, which disappears as the inflorescence gets older. The female

flowers are mature some time before the male, so that if the insect bears pollen from another individual it will in its wanderings effect cross-pollination. In escaping, the Fly must pass the stamens of the male flowers which have now dehisced, so that it becomes coated with a fresh load of pollen.

In many flowers, whose construction favours cross-pollination, eventual self-pollination takes place, as already noticed in Compositæ (p. 463 and Fig. 312, F). Other examples are afforded by the Canterbury Bell (*Campanula*) and Willow Herb (*Epilobium*). Certain plants produce flowers which are only capable of self-pollination, since they never open. Such *cleistogamic flowers* have minute unattractive petals and form very little pollen. Those of the Violet and Wood Sorrel (*Oxalis*) are produced after the showy flowers (which in the Violet are capable only of cross-pollination, cf. p. 461) and, owing to their short peduncles, remain hidden amongst the foliage-leaves. They are developed in the summer, when the trees above these woodland-plants have formed a dense crown of foliage, so that the light which reaches them is of relatively low intensity.

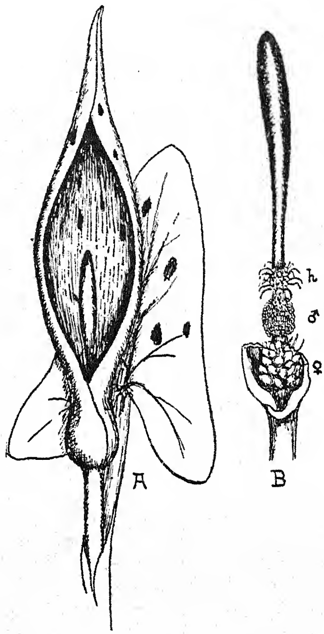

FIG. 328. Inflorescence of Cuckoo-pint (*Arum maculatum*) (slightly reduced). A, Leaf with complete inflorescence showing the bract. B, Spike with bract removed. *h*, hairs; ♂, male flowers; ♀, female flowers.

Our study of pollination has shown that, by contrast with the usually protective and relatively uniform calyx, the corolla exhibits great variety of form, and not only renders the flower conspicuous to insects, but usually shows obvious modifications to ensure the effectiveness of their visits and the exclusion of undesirables. The relative positions occupied by the floral leaves, and especially the extent to which they form a tube with or without fusion, play no small part in determining the nature and efficiency of the pollinating agent. It is thus mainly the latter that gives the clue to floral structure, whether the agency be insects, wind, or water. Plants developing the most effective mechanism will tend to set the greatest amount of seed and produce the most offspring.

Moreover, the increased certainty of pollination, where insects are the transferring agents, allows, except in pollen-flowers, of a reduction in the number of stamens and in output of pollen—in other words, an economy of material. Such specialisation, if extreme, may however defeat its own ends by unduly restricting the variety of pollinating insects.

[For further details regarding pollination, see P. Knuth, *Handbook of Flower Pollination* (Engl. transl. by J. R. Ainsworth Davis), 3 vols., Clarendon Press, Oxford, 1906–1909; and F. E. Clements and F. L. Long, *Experimental Pollination*, Carnegie Instit., 1923 (274 pp.), which contains a useful historical summary and an account of recent experimental methods for studying pollination. See also the work of J. C. Willis cited on p. 603.]

CHAPTER XXXVII

FERTILISATION AND EMBRYO-DEVELOPMENT

SINCE the ovules of Angiosperms are enclosed, the pollen cannot reach the micropyle direct as in Gymnosperms, but is received by the special receptive surface of the carpel, the *stigma*. This bears

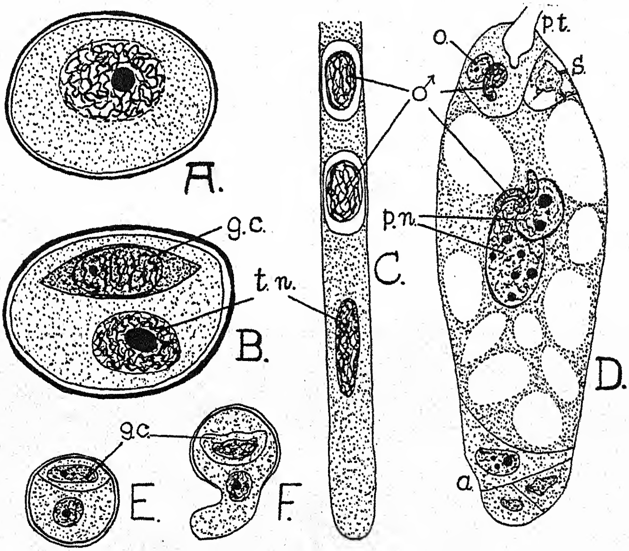

FIG. 329. Germination of pollen and fertilisation. A–D, *Lilium* (after Guignard). E–F, *Tulipa* (after Ernst). A, Mature pollen grain, showing the single nucleus. B and E, Later stage, showing generative cell (*g.c.*) and tube nucleus (*t.n.*). C, Tip of pollen tube with tube nucleus (*t.n.*) and two male cells (♂). D, Embryo sac at the moment of fertilisation, showing antipodals (*a.*), polar nuclei (*p.n.*), ovum (*o.*), one synergid (*s.*), and the two vermiform male cells (♂) discharged from the tip of the pollen tube (*p.t.*). F, Early stage in formation of pollen tube.

numerous papilla-like hairs, whose secretion nourishes the developing pollen. Before the pollen grain is shed its nucleus divides into two [1] (Fig. 329, B). One of these becomes surrounded by

[1] For further details, see the work by Coulter and Chamberlain cited on p. 437.

denser cytoplasm (*generative cell, g.c.*), whilst the other (*tube nucleus, t.n.*) lies freely in the general body of the grain. In this condition the pollen is transferred to the stigma, and here germination takes place (Fig. 329, F). The tube nucleus passes into the tip of the pollen tube, and the naked generative cell sooner or later follows suit (Fig. 329, C). The former usually remains undivided, whilst the latter ultimately produces two male nuclei.

In its downward growth the *pollen tube* is sometimes nourished by secretions from papillæ forming a continuous lining to the canal or canals traversing the style and extending uninterruptedly into the loculi of the ovary (*e.g.* Tulip and Violet). Often, however, the style is solid, the pollen tube penetrating through the axial core of thin-walled tissue, nourished by the sugary sap which the tissue contains. In some cleistogamic flowers (*e.g.* Purple Deadnettle) the pollen grains germinate in the anthers, and the pollen tubes grow from there to the stigma.

The period of time occupied by the pollen tube in growing down to the ovules varies greatly in different species, and bears no relation to the distance to be traversed. In the Crocus, where the style is 6–10 cm. long, the interval is only from one to three days, whilst in the Meadow Saffron (*Colchicum*), with a style of about the same length, it is six months (from autumn, when pollination occurs, to the following spring). A similar prolonged interval not uncommonly obtains in woody plants (*e.g.* Hazel), though the distance traversed is short, and in some Oaks the ovules do not even commence development until after pollination. In most spring-flowering plants the anthers develop as far as the mother-cell stage in the previous autumn, although in the Hazel ripe pollen can be found in the male catkins during midwinter.

As a general rule the pollen tube traverses the cavity of the ovary, and thus reaches the micropyle of one of the ovules (porogamy, Fig. 330, A). But, in certain trees and shrubs (*e.g.* Elm, Beech, Hazel), it grows through the placental tissue and enters the ovule near the chalazal end (chalazogamy, Fig. 330, B). The growth of the pollen tube may therefore be compared to that of a fungal hypha, and its power to penetrate tissues, and eventually the megaspore membrane, is doubtless due to an analogous secretion of digestive enzymes.

The downward growth of the pollen tube is mainly determined by a chemotropic stimulus due to substances contained in the ovules or in the ovary-wall. This fact can be experimentally demonstrated by sowing pollen grains of the Wild Hyacinth (*Scilla*) in a 5 per cent., or of *Echeveria retusa* in a 15 per cent., solution of cane-sugar around a fragment of the ovary, taking care to avoid

the inclusion of air-bubbles. The pollen tubes tend to grow in the direction of the piece of ovary.

Having passed through the micropyle, the pollen tube penetrates the overlying nucellar cap, and thus reaches the embryo sac. Meanwhile the generative cell has divided to form two *male nuclei* (Fig. 329, C, ♂), which are extruded from the tip of the pollen tube, and, entering the embryo sac, fuse respectively [1] (*a*) with the egg, and (*b*) with the two polar nuclei (cf. Fig. 329, D), or with the nucleus formed by the fusion of the latter. The former fusion

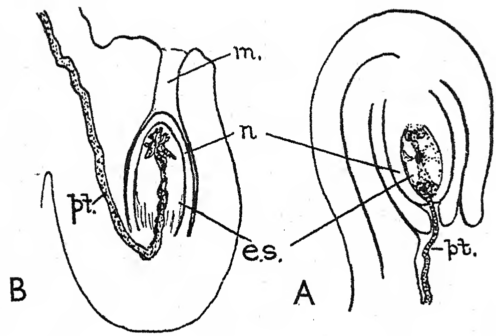

FIG. 330. Diagrams illustrating normal fertilisation (porogamy, A) and chalazogamy (B). *e.s.*, embryo sac; *m.*, micropyle; *n.*, nucellus; *pt.*, pollen tube.

results, in the usual way, in the production of an embryo, but the latter also leads to abundant division, whereby a nutritive tissue, the *endosperm*, is formed. In the utilisation of both male nuclei for these different purposes, Angiosperms exhibit a characteristic difference from Gymnosperms.

The product of the second fusion, which is really built up of three nuclei (one from either end of the embryo sac and one male nucleus), divides repeatedly, till the sac becomes filled with numerous free nuclei distributed uniformly throughout its protoplasmic content. Formation of separating walls now takes place almost simultaneously, so that the sac becomes occupied by a continuous thin-walled tissue, the endosperm, which stores food for the developing embryo.

During the nuclear divisions leading to endosperm-formation, the fertilised egg, now provided with a cell-wall, enlarges considerably and begins to segment. The first division is unequal, a smaller cell situated at the end away from the micropyle being cut off from the large remaining portion. The latter forms the sac-like

[1] This process is often spoken of as "double fertilisation."

basal cell (Fig. 331, I–VI, *b.*) and plays no further part in the development of the embryo. The smaller segment undergoes successive transverse divisions, so as to give rise to a short elongating *suspensor* (Fig. 331, *S.*). Hereby the slightly larger hemispherical terminal cell (*e.*), which subsequently produces the embryo proper,

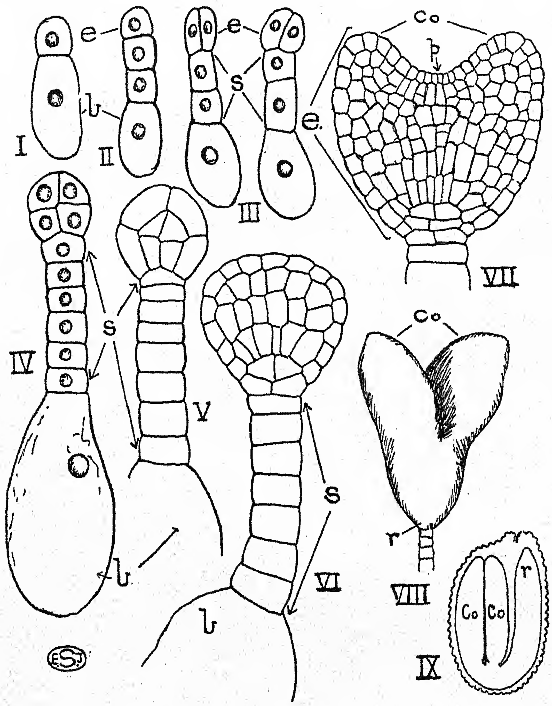

FIG. 331. Embryology of the Shepherd's Purse (*Capsella bursa-pastoris*). The successive stages are numbered I–IX. In VII and VIII only the embryo and a small part of the adjacent suspensor are shown. IX is a longitudinal section of a mature seed, showing the bent embryo. *b.*, basal cell; *Co.*, cotyledons; *e.*, embryo; *p.*, plumule; *r.*, radicle; *S.*, suspensor.

is carried down into the heart of the developing endosperm. Young *pro-embryos* at this stage of development, with a suspensor composed of a number of flat cells, are readily squeezed out of very young seeds of the Shepherd's Purse, such as can be removed from the ovaries of flowers which have not yet faded; the seeds are best mounted in water, and sudden pressure applied by tapping the cover-glass.

More advanced stages can be obtained in the same way from progressively older seeds. These show rather longer suspensors

and an increasing number of divisions in the enlarging embryonal cell (Fig. 331, IV–VI). The latter soon segments into octants, by three walls at right angles to one another (III, IV), and subsequent walls parallel to the surface (V, VI) delimit the future epidermis, cortex, and vascular system. Meanwhile the embryo assumes a more or less flattened form, and, at its wider free end, the future *cotyledons* appear as two lobes (VII, *Co.*) between which the *plumule* (*p.*) develops. The attached end of the embryo invariably becomes the *radicle* (VIII, *r.*), which thus faces towards the micropyle. Such embryos are to be found in seeds from almost ripe fruits (cf. IX).

The general method of embryo-development just described is that characteristic of a large number of Dicotyledons, although there are numerous differences in detail which are beyond the scope of this book. In Monocotyledons (Fig. 332, A–E), where the suspensor is often a more bulky structure (cf. especially Fig. 332, G), the single cotyledon (*Co.*) occupies the terminal position, whilst the plumule (*p.*) arises towards one side. Pro-embryos with a bulky suspensor are also found in some Leguminosæ (Fig. 332, I). It will be noticed that the embryos of Gymnosperms and Angiosperms do not develop a special absorptive organ (foot), such as characterises those of Bryophyta and Pteridophyta, although sometimes haustorial outgrowths arise from the suspensor.

The stimulating effect of fertilisation is not confined to the embryo, but also affects the ovule as a whole and the enveloping ovary, whilst even adjacent parts of the flower may undergo considerable enlargement and change (cf. p 478). The seeds are often many times the size of the ovules from which they sprang (*e.g.* Pea, Bean, etc.). The enlarged ovary-wall becomes the *pericarp*, and the integuments, or integument, form the *testa*. The character of the latter varies enormously, both as to its surface, which is often sufficiently distinctive in its sculpturing (*e.g.* Corn Cockle, *Agrostemma*) to serve for purposes of identification, and as to its durability and thickness. The embryo may absorb all the food-materials in the endosperm before entering upon its resting-stage (non-endospermic seeds, *e.g.* Pea), or part of the endosperm may persist until germination (endospermic seeds, *e.g.* Castor Oil, most Monocotyledons). In a few plants (*e.g.* many Caryophyllaceæ) the nucellus is not entirely replaced by the endosperm; in such a thin layer (*perisperm*) persists, even in the ripe seed, and functions for the storage of food. The degree of differentiation attained by the *embryo*, at the time when it enters upon its resting-stage, varies considerably. Thus, in the Runner Bean, even the venation of the first pair of plumular leaves is distinguishable. In the Castor Oil

the plumule is merely a peg-like structure, whilst in the Lesser Celandine (*Ficaria*) and Orchids (Fig. 332, H) the entire embryo is an undifferentiated mass of cells, a condition likewise encountered in the embryos of most parasites. In some plants, moreover, there

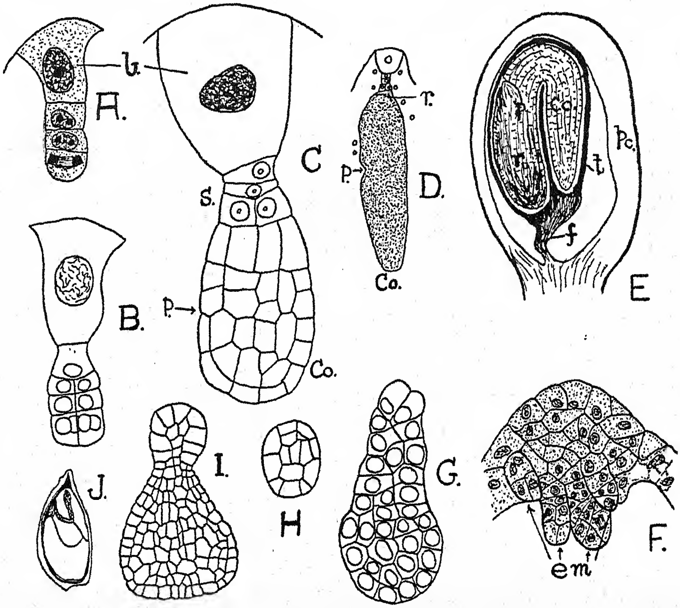

FIG. 332. Embryology of various plants. A–D, Successive stages in the development of the embryo of the Arrowhead (*Sagittaria*) (after Schaffner). E, Longitudinal section of ripe achene of the Water Plantain (*Alisma*) (original). F, Formation of several embryos (*em.*) from a massive suspensor, by budding, in *Erythronium americanum* (Liliaceæ) (after Jeffrey). G, Pro-embryo, with massive suspensor, of *Lilium* (after Coulter). H, Embryo of Twayblade (*Listera ovata*), at time when seed is shed (after Pfitzer). I, Pro-embryo of *Spartium junceum* (Leguminosæ) (after Guignard). J, Longitudinal section of Orange pip (*Citrus*) (with two embryos) (after Wettstein). *b.*, basal cell; *Co.*, cotyledon; *f.*, funicle; *p.*, plumule; *pc.*, pericap; *r.*, radicle; *S.*, suspensor; *t.*, testa.

is no resting period (*e.g.* in the tropical Mangroves), whilst in many trees the seeds germinate most readily if sown immediately on reaching maturity.

Exceptions to the normal sequence of events described in the foregoing pages are by no means uncommon. *Apogamy* (cf. p. 385), for example, has been recorded in quite a large number of Compositæ (*e.g.* Dandelion, Hawkweed), as well as in some species of Lady's Mantle (*Alchemilla*), which produce seed without fertilisation. Here the reduction division does not appear to occur, and the embryo

arises from an unfertilised cell of the embryo sac having the diploid number of chromosomes. Such apogamy is of course akin to vegetative propagation, but gains the advantages afforded by the mechanism for seed-dispersal. Despite the non-occurrence of a sexual process in such apogamous forms, pollination sometimes appears to furnish a necessary stimulus for embryo-formation. More rarely it is an ordinary cell of the nucellus that divides to form the embryo (e.g. *Citrus*), a condition analogous to the *apospory* described among Ferns (p. 384). In the Hawkweeds (*Hieracium*) all three conditions—apogamy, apospory, and normal fertilisation—have been observed.

The occasional presence of more than one embryo within a seed may be due to several causes. Sometimes more than one member of the tetrad, formed by the megaspore mother-cell, develops into an embryo sac, so that several embryos can exist from the first. But more frequently accessory embryos arise by vegetative budding from the pro-embryo (Fig. 332, F). Orange pips frequently contain several embryos, of which one is the outcome of a sexual fusion, whilst the others are derived from nucellar cells which are presumably stimulated to growth as a result of fertilisation (Fig. 332, J).

The general course of the life-history in Angiosperms is obviously very similar to that of Gymnosperms. In both the young embryo lives, as a parasite, within the ovule, which forms a protective envelope around it until the time of germination. As with the young Fern, however, its independence is soon established. In contrast to Gymnosperms, the most striking features are connected with the very efficient arrangements for the protection and nourishment of the developing embryos and seeds, and the highly perfected mechanism for pollination by virtue of which the most intimate relation often obtains between the flower and the pollinating agent.

CHAPTER XXXVIII

FRUITS, SEEDS, AND DISPERSAL

As a result of fertilisation the wall of the ovary enlarges and usually becomes either hard and dry, or fleshy, thus giving rise to the *pericarp*, the fruit itself being described as dry or succulent according to the character of its wall. It will be realised, therefore, that the fruit corresponds to the whole ripened ovary, whilst the seeds are the matured ovules contained within it. When there is any doubt as to the nature of a given structure (*e.g.* in Gramineæ, where the testa of the single seed is completely joined up with the pericarp, cf. p. 29), a seed can always be distinguished from a fruit by the fact that it exhibits only one scar (the hilum, p. 21), whereas the fruit shows two, one marking the former attachment to the plant, the other the remains of the style.

Where the ovary is syncarpous a *simple fruit* develops from it, but when the ovary is apocarpous each carpel matures separately and the aggregate is a *compound fruit*. Two types of dry fruits may be distinguished, the one usually remaining attached to the parent-plant and splitting open to liberate the contained seeds (dehiscent fruits), whilst in the other the fruits are detached and the pericarp merely decays away (indehiscent fruits). Practically all indehiscent fruits are one-seeded, whilst many-seeded ones are dehiscent. The necessity for dehiscence in the latter class is obvious, since otherwise all the seeds would come to germinate at the same spot and the offspring would harm one another by mutual competition.

Examples of *dry indehiscent fruits* are furnished by *achenes* with a membranous, and *nuts* with a hard woody pericarp. The fruit of Compositæ and Gramineæ is an achene which is peculiar in the fusion of pericarp and testa. That of the Buttercup (Fig. 333, *a*) consists of a collection of achenes. The Hazel and the Acorn provide instances of nuts, each of which is enclosed in a cupule [1] formed by joined bracts and bracteoles, but it may be mentioned

[1] This forms the cup of the Acorn and the prickly covering of the fruits of the Sweet Chestnut (*Castanea*).

that some of the nuts of commerce (*e.g.* Walnut, see p. 478, Brazil Nut) are not true nuts.

Not uncommonly fruits derived from multilocular ovaries, containing more than one ovule, split along the septa into compartments, each with a single seed and equivalent to as many achenes; such fruits are said to be *schizocarpic*. Thus, in the Umbelliferæ the fruit at maturity splits into two achenes (Fig. 334, A), whilst

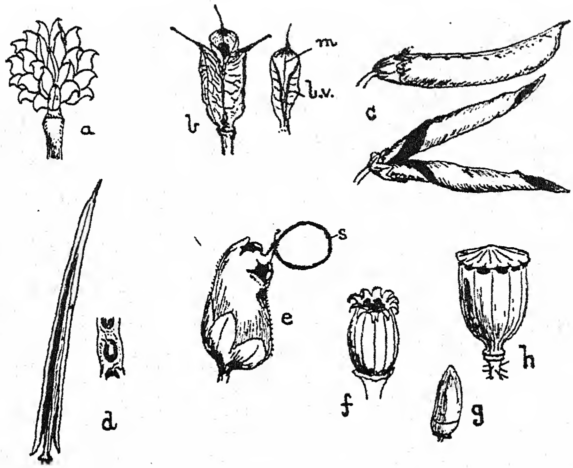

FIG. 333. Examples of dry fruits (*a* and *d*, natural size; *g*, somewhat enlarged; others slightly reduced). *a*, Buttercup (collection of achenes). *b*, *Aconitum* (three follicles). *m*, midrib of carpel; *l.v.*, lateral vein of same. *c*, *Vicia* (legume); lower figure shows pod after dehiscence. *d*, Wallflower (siliqua); right-hand figure shows portion of false septum with seeds. *e*, *Antirrhinum* (capsule with apical pores). *s*, style. *f*, Campion (capsule with teeth). *g*, Plantain (capsule with lid). *h*, Poppy (porous capsule).

the Labiatæ exhibit four achenes (Fig. 334, D) produced by an early fission of the ovary, and the Mallow (Fig. 334, C) as many achenes as there were loculi in the original ovary. A similar splitting of the ripe fruit into compartments is seen in the Crane's Bill (Fig. 334, B), but here the contained seeds are subsequently shot out of the opening segments.

The simplest type of *dehiscent fruit* is the *follicle*, seen in the Marsh Marigold, Monkshood (Fig. 333, *b*), etc., in which the dry pericarp formed from a single carpel dehisces along the ventral suture (p. 440). This constitutes the most essential difference from the *legume* of Leguminosæ (Fig. 333, *c*) in which dehiscence takes place along both sutures, the two valves often twisting when ripe. A somewhat similar fruit is the *siliqua* characteristic of Cruciferæ (*e.g.* Honesty, Wallflower, Fig. 333, *d*). Here dehiscence

takes place along both edges and commences at the base of the elongated fruit, so that the two carpels separate from below but remain cohering above. The septum (p. 442), spread out on a framework formed by the parietal placentas, remains standing vertically and the seeds attached to the latter (cf. right-hand drawing in Fig. 333, *d*) are gradually shaken off by the wind. Many members of the Cruciferæ have very short siliquas known as *siliculas* (*e.g.* Shepherd's-purse, Fig. 4, B) which dehisce in just

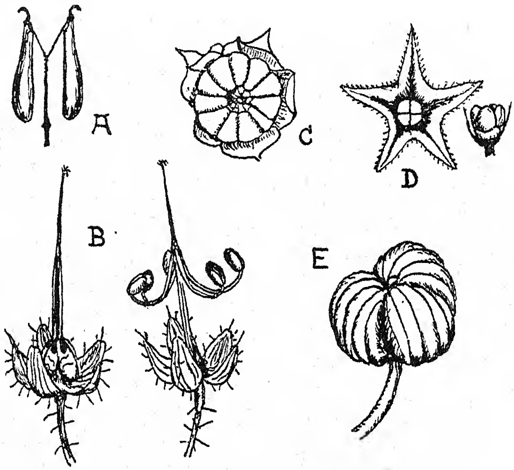

FIG. 334. Types of schizocarpic fruits (A enlarged, other figures natural size). A, *Anthriscus*. B, Crane's Bill (*Geranium*); left-hand figure before, right-hand figure after, splitting into achenes. C, Mallow. D, White Dead-nettle; right-hand figure shows fruit, with calyx removed, in side-view. E, *Tropæolum*.

the same way. All dehiscent fruits arising from a syncarpous ovary are described as *capsules*, the siliqua just mentioned being a special form of the latter.

Capsules differ chiefly amongst one another in the number of compartments and the mode of dehiscence. Most commonly opening takes places by longitudinal slits in the pericarp along the dorsal suture of each carpel (*loculicidal*, *e.g.* Iris, Willow-herb), whilst much more rarely the slits appear along the lines of junction of the carpels (*septicidal*, *e.g.* St. John's Wort). In the Caryophyllaceæ and the Primrose the top of the unilocular fruit splits into a number of teeth which curl right back in dry air (Fig. 333, *f*), whereas in the Pimpernel (*Anagallis*), Henbane, and Plantain (Fig. 333, *g*) it breaks off cleanly as a lid. The ripe fruit of the Poppy (Fig. 333, *h*) exhibits a series of pores beneath the flat top (*porous dehiscence*), due to the wall between each pair of placentas curling slightly outwards at these points; pores are formed in a similar manner at the base of the hanging capsule of the Harebell. In *Antirrhinum* (Fig. 333, *e*) there are three openings at the apex of the fruit, each of which is surrounded by several small teeth.

The Crane's Bill (Fig. 334, B) shows that even one-seeded compartments may dehisce, and the same is observed in the Horse Chestnut in which the prickly pericarp splits into three valves at maturity. The fruit of this tree, however, sometimes includes two or even three seeds, so that dehiscence is advantageous. The occasional presence of more than one seed is due to the fact that each of the three loculi of the ovary contains two ovules, although as a general rule only one of the six ripens. The majority of indehiscent fruits are one-seeded from the first, but in some this condition is attained, as in the Horse Chestnut, by all but one of the ovules dying away; thus the ovary of the Oak is trilocular with two ovules in each compartment, but five of these invariably fail to ripen, leaving the Acorn one-seeded.

The two principal types of *fleshy fruits*, both indehiscent, are the *berry* and the *drupe*. The former has a pericarp which is

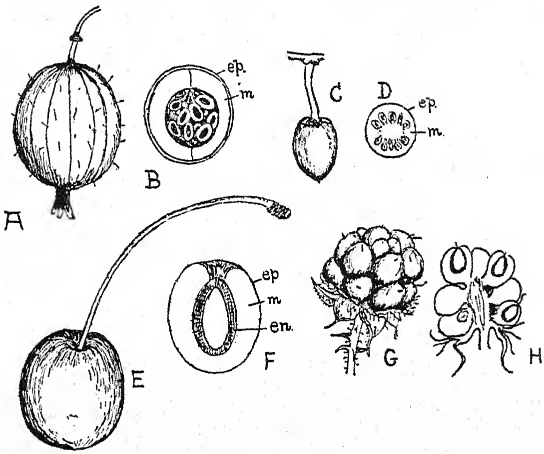

FIG. 335. Types of fleshy fruits (slightly reduced). A–B, Gooseberry (*Ribes grossularia*), entire and in cross-section. C–D, Bittersweet (*Solanum dulcamara*) (berry), entire and in cross-section. E–F, Cherry (drupe), entire and in longitudinal section. G–H, Blackberry (collection of drupes), entire and in longitudinal section. *en.*, endocarp; *ep.*, epicarp; *m.*, mesocarp.

fleshy throughout, whilst in the latter the inner part is hard and stony. We can, consequently, in the berry (Fig. 335, A–B) distinguish between the surface-skin or *epicarp* (*ep.*) and the fleshy portion or *mesocarp* (*m*), whilst in the drupe (Fig. 335, E–F) we have in addition the hard *endocarp* (*en.*). Examples of berries are furnished by the Currant, Gooseberry (Fig. 335, A–B), Bittersweet (Fig. 335, C–D), and Tomato, the first two having parietal (Fig. 335, B), the last two axile placentas (Fig. 335, D). The Date (*Phœnix*) is a single-seeded berry in which the hard stone is constituted by the endosperm, the actual testa forming the delicate membrane around the latter. Other special kinds of berries are

the Orange, Lemon, Grape, Banana, Cucumber, and Vegetable Marrow. In the two first the fleshy part is constituted by succulent hairs which are outgrowths of the carpel walls, while the Banana is a berry that is seedless in the cultivated varieties.

Typical drupes are the Plum, Cherry (Fig. 335, E–F), Almond, Peach, etc., whilst the Walnut (*Juglans*) and Coco-nut are drupes in which, however, the layers outside the endocarp are generally removed before they are placed on the market. The Raspberry and Blackberry (Fig. 335, G and H) furnish instances of compound fruits (p. 474) composed of many small drupes. Whereas berries are generally many-seeded, drupes usually contain but one seed. The hard endocarp renders the drupe equivalent to a nut, while the individual seeds of a berry get scattered when the fruit is eaten by animals.

In some plants the fruit is not composed of the ovary alone, other parts of the flower (especially the receptacle) participating in its formation, when we speak of it as a *false fruit*. Thus, in the Strawberry (Fig. 336, D) the true fruit consists of a number of minute achenes (*a*), but these are carried up on the much enlarged and fleshy receptacle (*r*) which constitutes the actual edible part. In the Apple (Fig. 336, E) and Pear the flesh is formed by the receptacle (*r*) in which the inferior ovary (the core, *ov.*) is embedded. The hip of the Rose (Fig. 336, C) is another false fruit in which the coloured flask-shaped envelope develops from the deeply hollowed thalamus (*r*), whilst the fruit proper is constituted by the contained achenes (*a*).

Some false fruits are formed from complete inflorescences. In the Mulberry (Fig. 336, A) the individual fruits are achenes, each covered by four fleshy perianth-members (*p*). The Fig (Fig. 336, B) originates from a peculiar inflorescence in which the fleshy axis (*a.i.*) is deeply hollowed out, the cavity being lined with numerous minute flowers.[1] The Pineapple (*Ananas*) is likewise an entire inflorescence.

Many young fruits are protected by the persistent calyx (*e.g.* Caryophyllaceæ, Fig. 422, E, and Labiatæ, Fig. 334, D), whilst in Compositæ the same function is fulfilled by the involucre (p. 428). In mature fruits, which have dehisced, the seeds are often shielded during wet weather by a more or less marked closing of the valves; thus, in the Caryophyllaceæ the teeth at the top of the capsule (Fig. 333, *f*) come together when the air is damp, a feature due to unequal absorption of moisture by their two sides.

[1] Considerable information on fruits of tropical plants will be found in H. F. Macmillan, *Tropical Planting and Gardening*, Macmillan & Co., 4th edit., 1935 (560 pp.), a useful illustrated reference-book on cultivated plants of the Tropics.

Far more important than an enumeration of the characters of fruits is the relation which these bear to the *dispersal*[1] of the seeds. Nearly all plants produce far more seeds than can ultimately survive, the bulk of the seedlings being killed off as the result of competition with more successful ones. This can be observed in any seed-bed that has been too densely planted, but one sown with mixed seed will support a considerably greater

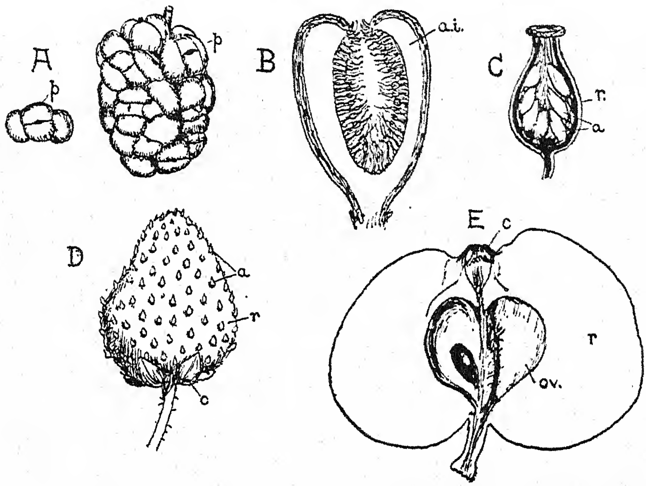

FIG. 336. Examples of false fruits (slightly reduced). A, Mulberry (*Morus*); single fruit shown on left. B, Fig (*Ficus*), in longitudinal section. *a.i.*, axis of inflorescence. C, Hip of Rose, in longitudinal section. D, Strawberry (*Fragaria*). E, Apple, in longitudinal section. *a*, achenes; *c*, calyx; *ov.*, ovary; *p*, perianth-member (in A); *r*, receptacle.

number of individuals. Reproduction by seeds is superior to vegetative multiplication, owing to the fact that seeds are usually carried some distance from the parent. A large proportion of the seeds shed by a plant will, however, be carried to situations unsuitable for a further development. In view of this great mortality it is of advantage that a plant should produce numerous seeds and that these should be widely scattered, since in this way some are certain to reach a suitable situation and the risk of competition with the parent or with one another is diminished. For most plants wind or animals[2] are the agents of seed-dispersal.

A very simple feature facilitating *wind-dispersal* consists in the production of minute and light seeds (*e.g.* Foxglove) an extreme

[1] For a detailed treatment, see H. N. Ridley, *The Dispersal of Plants*. L. Reeve, 1930 (744 pp.).

[2] Regarding dispersal by water, see p. 554.

instance being seen in the Orchids in which they form a powdery mass. Many other plants, however, propagate by light seeds of small size, which are capable of being carried considerable distances by the wind. In most of these the fruits are attached to the plant in such a way that the seeds are readily shaken out. Thus, in the Harebell the hanging fruits are disturbed by every breeze (censer-mechanism) and, in their oscillations, the seeds are gradually dispersed through the pores of the capsule. In many Caryophyllaceæ and the Poppy (Fig. 333, *e*, *f*, *h*), the ripe fruits are borne at the ends of stiff upright elastic peduncles which bend with sudden gusts of wind and then spring back to their normal position, thus shooting out some of the seeds like a catapult.

In a number of plants (*e.g.* Gorse, *Impatiens*) the different layers of the pericarp dry to an unequal extent during ripening, so that a tension is created which leads, at the slightest touch, to an explosive rupture of the fruit, the seeds being projected some little distance.

An expansion of the pericarp in the shape of a *wing* often helps in the distribution of one-seeded fruits, good instances being afforded by the Ash (Fig. 337, A) and the Elm. Similarly, in the Sycamore (Fig. 337, B) the ripe schizocarp splits into two winged achenes. Each group of fruits in the Lime (Fig. 337, C) is suspended from the middle of a strap-shaped bract (*br.*) which aids in dispersal. A similar co-operation of bracts in fruit-distribution is seen in the Hornbeam (*Carpinus*, Fig. 419, C). Winged seeds are rarer, but are found, for instance, in the Field Spurrey (*Spergula arvensis*) and Honesty (*Lunaria*).

The pericarp or testa is often produced into hairs. Good examples of such *plumed* seeds are seen in the Willow and Willow-herb (Fig. 337, D), both of which have capsules. In *Clematis* (Fig. 337, F) and *Anemone pulsatilla* the style of each achene is feathery and enlarges after fertilisation to form a plume. In the Compositæ the calyx of the individual florets is usually developed as a number of fine hairs (*pappus*) arising from the top of the inferior ovary (cf. p. 433, and Fig. 312, B and C), thus forming a plumed fruit. These hairs form a kind of parachute by means of which the achenes drift readily in the air; when, as in *Tragopogon*, the hairs of the pappus are themselves feathery, they are still more effective. In the Dandelion (Fig. 337, E) and *Tragopogon* a long stalk (*s*) develops after fertilisation between the pappus and the ovary.

The individual hairs of the pappus spread out more or less horizontally when the air is dry, but close together vertically when it is damp. Thus, the fruits are only dispersed under favourable conditions, whilst, when once on the wing, they fall to the ground

with the advent of rainy weather, during which they are likely to become washed into the soil.

Succulent fruits depend for their dispersal on animals. Their adaptational features are the usual bright colouring, the fleshy edible character of part or whole of the pericarp, and the protection

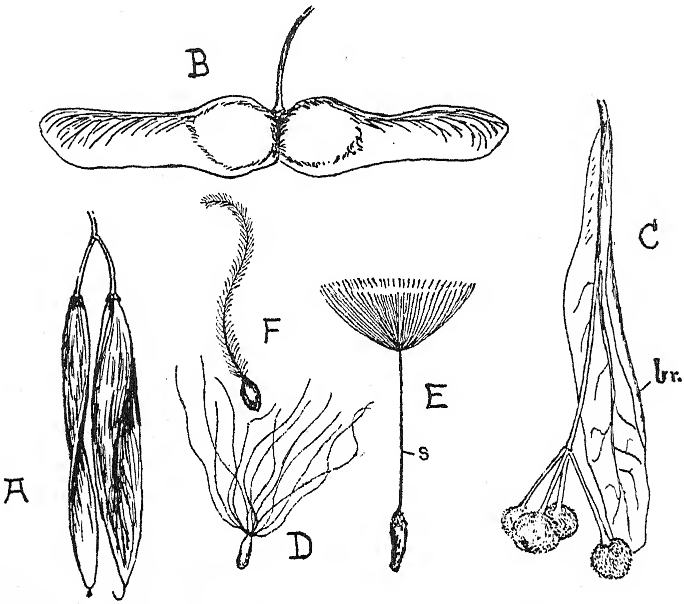

FIG. 337. Winged and plumed fruits and seeds (all natural size). A, Ash (*Fraxinus*) (two winged achenes). B, Sycamore (*Acer*) (schizocarpic, splitting into two winged achenes). C, Lime (*Tilia*). *br.*, bract. D, Plumed seed of Willow-herb. E, Dandelion (*Taraxacum*) (achene with superior pappus). *s*, stalk. F, *Clematis* (achene with feathery style).

of the seed-contents of all these fruits by a hard covering furnished either by the endocarp (drupes) or the testa (berries). As a consequence of the last feature, such seeds are able to pass through the digestive tracts of animals without the embryo coming to harm, the seed being deposited with the fæces; thus a certain amount of manure is available for the seedling which subsequently develops. It may be noted in this connection that the seeds of the Hawthorn (*Cratægus*) and others, which are normally swallowed and pass through the alimentary tract of animals, germinate much more readily after having been acted upon by the gastric juices. Even when the stone is not swallowed, the bird or other animal generally carries the fruits some little distance from the parent before dropping

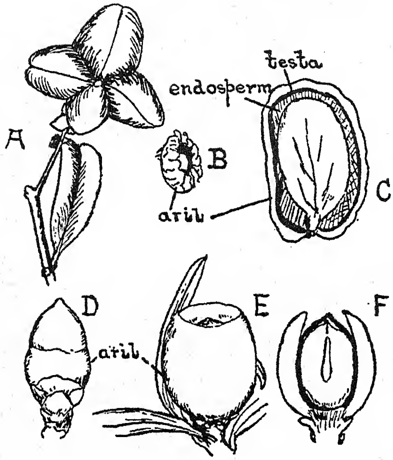

FIG. 338. Seeds of the Spindle-tree and Yew (C considerably enlarged, other figures natural size). A–C, Spindle-tree (*Euonymus*). A, Single fruit. B, Young seed with aril. C, Ripe seed in longitudinal section. D–F, *Taxus*. D, Young seed. E, Older seed. F, Ditto in longitudinal section.

the seeds. In the Mistletoe part of the flesh of the fruit is very sticky, so that the contained seed adheres to the bill of the bird who rubs it off on to the branch of a tree; the seedling is thus from the first attached to the plant on which it lives (p. 217).

Fleshy seeds are rare in our country. In the Spindle-tree, the single seed found in each of the four compartments of the fruit (Fig. 338, A) is enveloped by a bright-orange puckered envelope (*aril*, Fig. 338, B and C) which is very conspicuous when the capsule dehisces. Another example is furnished by the Yew (Fig. 338, D, E). In these two forms the seeds are distributed by Birds, but in the Gorse, whose seeds have a small fleshy swelling at one end, Ants are stated to act as the agent of dispersal.

A considerable number of low-growing herbs develop hooks on their fruits or on adjacent parts of the flower, and such *burr-fruits* are usually distributed by hairy animals. Thus, in Cleavers (*Galium aparine*) and *Circæa* (Fig. 339, B) the hooks are borne on the fruits themselves, whilst in *Geum* (Fig. 339, D) a portion of the style of each achene forms a long stiff claw. On the other hand, in the Burr Marigold (*Bidens*, Fig. 339, C) it is the calyx that is modified, the customary pappus being here replaced by two or three stiff bristles with backwardly directed barbs. The top part of the

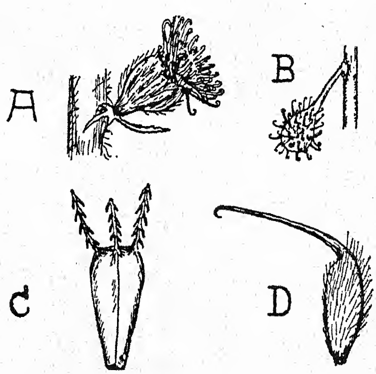

FIG. 339. Types of burr-fruits (A and B, natural size; C and D somewhat enlarged). A, *Agrimonia* (hooks on receptacle). B, Enchanter's Nightshade (*Circæa*) (hooked fruit). C, Burr Marigold (*Bidens*) (hooked calyx). *D, Geum* (hooked style).

receptacle of the Agrimony (Fig. 339, A), again, is beset with numerous hooks, whilst in the Burdock (*Arctium*) the involucre is similarly equipped. Seeds, which become sticky when wet (*e.g.* Plantain, Chickweed), may adhere to bird's feathers and so be dispersed.

We have already on p. 20 described the general way in which fruits and seeds get buried in the soil. In the Stork's Bill (*Erodium*) the segments of the style, which separate with the indehiscent achenes of the schizocarpic fruit (as in Fig. 334, B), coil up when dry, but uncoil when moist; a similar behaviour is shown by the awns (p. 625, and Fig. 439, A, *a*) on the fruits of the Oat (*Avena*). Since the hairy or rough surface of the awn causes it to cling to the soil, its extension, when the latter is damp and consequently soft, results in the fruit being driven into the ground.

CHAPTER XXXIX

THE PLANT-ENVIRONMENT

WE have so far considered plants separately, that is, as isolated individuals, but in nature they generally grow together in communities, the separate members of which not only mutually affect one another, but have to accommodate themselves to all the circumstances of their surroundings. These collectively, that is to say both the physical conditions, due to soil and climate, and the biotic conditions produced by other plants and animals, constitute what is termed the *environment* of the plant. The nature of this environment is in fact the result of present conditions, but it is also to a considerable extent the outcome of its past history. Moreover, the biotic conditions are not fixed, partly because plants themselves modify their environment and also because they are markedly plastic. The situation in which a plant grows, having regard to all the conditions of its environment, is termed its *habitat*, and the study of the relation of plants to their environment and to one another is termed *ecology*.

The various conditions afforded by the environment are spoken of as the *habitat factors*, and these may be grouped into several categories. For instance, the conditions determined by soil are the *edaphic* factors, while those due to surface changes are the physiographic factors. There are also climatic and historic factors, as well as *biotic* factors, the latter depending upon the influence of other plants and animals. It is important to realise that these groupings though convenient are rather arbitrary, since different factors interact with one another. Thus changes in topography, such as increase of altitude, affect climatic conditions, whilst the influence of soil on vegetation varies according to the climate with which it is associated. So too a biotic factor (*e.g.* shading of one plant by another) may vary in its effect, according as the water supply is high or low, whilst the species of plants making up a community will be determined in no small degree by the past history of the area concerned.

The *climatic factors* comprise temperature, precipitation,

humidity, wind, and light. Of these temperature is particularly significant, if the world as a whole is considered, while in more limited areas it is important with respect to seasonal changes and the length of the growing season, especially when there are marked differences in altitude. Rainfall, humidity, and temperature are obviously interrelated, since the higher the temperature and the greater the saturation deficit of the air the less will be the effective value of any particular rainfall. Since precipitation is chiefly important by reason of its supplying moisture to the plant, it is evident that the seasonal distribution of rainfall is more significant than its total annual amount, and with respect to this as to other factors it must be emphasised that the extreme conditions may influence plant growth far more than the average. Precipitation during the growing season has more importance than that which falls during the period of rest, whilst periodic droughts may alter the character of the plant-covering (*e.g.* some deserts), despite adequate water supply during intervening periods. Amongst the climatic factors rainfall is of prime importance.

Wind by its drying action accentuates any tendency towards water-shortage and prevents the growth of plants with high water-requirements. Its velocity increases with height, so that tall vegetation requires more water or must have a greater resistance to desiccation, as well as needing greater mechanical strength. The effect of wind is especially marked on wind-swept coasts (Ch. XLV) and at high altitudes (p. 528).

Light, though comparatively uniform over large areas of the earth's surface, varies markedly in intensity with latitude and from one part of the year to another, so that a degree of shading that is tolerated in summer may well prevent growth in spring. Moreover, the duration of daily illumination exhibits similar changes (p. 247).

The effect of climate is well illustrated by the distribution of forest, grassland, and desert over the earth's surface. In general, forest occupies the regions of highest, and desert those of lowest, rainfall, whilst grassland occurs in areas of medium, rather uniformly distributed, rainfall; the influence of man or of winds may, however, profoundly modify the applicability of this generalisation. In northern latitudes forests are composed of such trees as Birch, Pine, and Spruce (*Picea*), whilst in temperate zones deciduous trees, such as Beech, Oak, and Ash, predominate. On the slopes of high mountains, like those of Switzerland, the same relative distribution occurs, with deciduous forests below and Coniferous ones above.

Amongst *biotic factors* the competition between different species or between individuals of the same species is most important. Plants, when free from competition, develop much more extensive

root-systems than when growing together, and their capacity to form root and shoot when associated together, varies both with the competing species and with the other habitat factors. Competition for light is one of the commonest aspects of the effect of plant on plant, as is especially evident in woodlands (cf. p. 519). The interaction between plants and animals involves both beneficial and non-beneficial relationships. Beneficial relationships are exemplified by the rôle of insects as pollinating agents and of other animals as agents in the dispersal of fruits and seeds. Moles, rabbits, and earthworms serve as natural cultivators of the soil. But, since animals are directly or indirectly dependent upon plants for their food, it naturally follows that animals often have a deleterious effect upon plants, influencing it may be the frequency of particular species or altering the prevalent physiognomy of the vegetation. Thus the grazing of herbivorous animals maintains grassland in areas that would otherwise become scrub or woodland (p. 531) and overstocking has in arid areas of Australia led to such depletion of the plant-cover as to result in soil erosion and desert conditions. In Britain and even more in less populated areas the rabbit has had a profound effect in checking plant-growth, especially with respect to seedlings of woody species. The ravages of Caterpillars may sometimes destroy a plant entirely in a small area (*e.g.* the Five-spot Burnet attacking Bird's-foot Trefoil), although such devastation by insects is much more extensive in warmer parts of the earth (*e.g.* by swarms of Locusts). Many plants possess some protection in the form of spines (cf. p. 507), of distasteful substances, of needle-like crystals, etc.

The presence of characteristic species in any particular type of situation is evidence of some benefit or benefits which they gain, either directly, through the nature of the soil or climate, or indirectly, through being relieved from the severity of competition with plants that, in other conditions, would prove more successful (cf. p. 519). But, whilst every habitat may be said to confer a benefit upon its legitimate inhabitants, it is equally true that adaptation to its special conditions is also involved, in particular to those conditions which are most pronounced. Thus, in any given locality that particular factor which most nearly approaches the minimum requisite for life or which is present in excess, whether it be water, light, temperature, or food-supply, will be that one which most profoundly affects the character of the vegetation. For, if the other essential conditions are amply sufficient for most, if not all, of the species present, the successful plants in the struggle for existence will be those best able to flourish under the particular extremes, either of deficiency or excess. The more

specialised the habitat, the more specialised must the plant be to survive there. Thus, the only forms that can live in a desert are plants that can withstand great water loss, while further examples are furnished by aquatics. It must be realised, however, that, although a certain plant may be eminently successful in conditions to which its structure is adapted, these very modifications may often render it unsuited to another environment (*e.g.* aquatics, succulents, cf. p. 510).

[Important general reference-works are: J. Braun-Blanquet, *Plant Sociology* (Eng. transl. by G. D. Fuller and H. S. Conrad), McGraw Hill Book Co., 1932 (439 pp.), which contains a good presentation of the more floristic aspects of plant geography; H. Lundegardh, *Environment and Plant Development* (transl. by E. Ashby), Ed. Arnold, 1931 (330 pp.), a useful account of the chief habitat factors; C. Raunkiaer, *Life-forms of Plants and Statistical Plant Geography*, Clarendon Press, 1934 (632 pp.); A. G. Tansley, *Practical Plant Ecology*, Allen & Unwin, 1923 (228 pp.); A. G. Tansley and T. F. Chipp, *Aims and Methods in the Study of Vegetation*, British Empire Vegetation Committee, London, 1926 (383 pp.); J. E. Weaver and F. E. Clements, *Plant Ecology*, McGraw Hill Book Co., 1929 (520 pp.); E. J. Salisbury, "The Geographical Distribution of Plants in relation to Climatic Factors," *Geographical Journal*, 1926, pp. 312–342. For ecological conditions in relation to garden plants, see E. J. Salisbury, *The Living Garden*, G. Bell & Sons, 1935 (338 pp.).]

CHAPTER XL

THE SOIL (EDAPHIC FACTORS)

THE soil from which the roots of plants derive so much of their nourishment is, considered physically, a more or less loose aggregation of two kinds of particles. On the one hand there are the mineral particles formed by the breaking down of rocks under the influence of atmospheric and other agencies; on the other hand there are the organic particles consisting of the decaying remains of plants and animals that have previously lived on the soil in question, such organic material being spoken of collectively as *humus*. This dead matrix is permeated by a soil-atmosphere and a soil-solution. In addition there is a teeming population of microscopic animal and vegetable organisms, some of which are essential to the well-being of the larger plants (p. 348).

The mineral particles, which usually exceed the organic in amount, depend in their nature on the kind of rock from which they have been derived. Thus, the soil in a sandstone or gravel area will tend to consist in the main of sandy particles, *i.e.* of relatively large grains of semi-transparent quartz which are, however, frequently coloured red or brown by iron-compounds. Similarly, in a chalk area we find a considerable proportion of chalk particles in the soil (calcareous soil), which in consequence is often conspicuous by its greyish-white colour. A mineral matrix of a more mixed character is found where the rocks are of volcanic origin (igneous rocks, *e.g.* granite, basalt, etc.), since these are composed of many different kinds of minerals (*e.g.* quartz, felspar, mica, and hornblende, the commonest constituents of granites).

In all these instances we are dealing with soils formed *in situ*, and there is thus, apart from such chemical changes as may have taken place, a close relation between the character of the soil and the nature of the underlying rock. But this need not necessarily be so. The material formed by the breaking down of rocks may be carried away by running water which, according to its rate of flow, has the power of transporting particles of varying size, and the latter are thus progressively deposited with the gradual decrease

in rapidity of the current. In this way there arise the gravel banks and the large stretches of alluvial soil, so commonly found near the mouths of rivers. Movement of glaciers during the Glacial Period has also been instrumental in the transference of material, and by the disintegration of the boulders, etc., transported upon the ice, large areas of clay and gravel have been produced (*e.g.* Hertfordshire Boulder clay, glacial drifts of Norfolk).

As a general rule the soils one meets with in nature are mixed soils in which, however, one kind of particle often predominates, pure soils being relatively rare. The structure of a soil may be studied as follows: One or two lumps of *unbroken* earth are first placed in a vessel of water and moved about to displace the air from their surfaces; if they now be broken up, bubbles arise from them showing the presence of air within the soil. The amount of this soil-atmosphere can be estimated in the following way.

A tin which must not leak is filled to the brim with water and completely immersed in a tall glass cylinder partly filled with the same liquid; the level of the water in the cylinder is then marked by a piece of gummed paper. The tin, still full, is removed, and after the moisture from its surface has been allowed to drip into the cylinder, the contained water is poured away and a number of holes punched in its base. Thereupon the open end is driven down into the soil *in situ*, until the tin is completely filled, after which it is dug out and the soil in the tin cut off flush with the top edge. The whole is now placed in the cylinder and the contained soil is scooped out under the surface of the water, so as to ensure complete displacement of the soil-air. The water in the cylinder now stands at a lower level than that previously marked by the paper. By adding water from a measuring-glass until the marked level is reached, we obtain an approximate estimate of the amount of air in the volume of soil used.

There must thus be a more or less considerable number of spaces in the soil which are occupied by soil-air (Fig. 340, *a*). The latter stands in connection with the atmospheric air and is continually circulating from one part of the soil to another, being of immense importance in the respiration of roots and of the organisms (*e.g.* Bacteria, Protozoa), which live near the surface. The soil-atmosphere differs, however, from that of the air in having a much higher proportion of carbon dioxide and less oxygen. Whenever the soil is dug up or otherwise worked, the amount of air in the interspaces increases, so that such soil occupies a larger volume than before. A correct estimation of the natural air-content can therefore only be obtained, if the method described in the last paragraph is adopted.

Since a considerable space in the soil is occupied by air, the question arises as to where the water is situated. If a small quantity of moist earth is spread out in a thin layer on a sheet of white paper, the individual particles have a fresh or glistening surface. The paper with the soil may now be dried and again examined, whereupon the particles appear dull. The glistening was due to a very thin film of water which coated each soil-particle and disappeared on evaporation. In a soil which is capable of supporting a healthy growth of plants, the moisture occurs mainly as such films (Fig. 340, *w*), which coalesce so as to fill the smaller interspaces, but surround the air in the larger ones. Most bodies after immersion in water show a similar film which is due to an adhesive force operating between the water and the surface of the body.

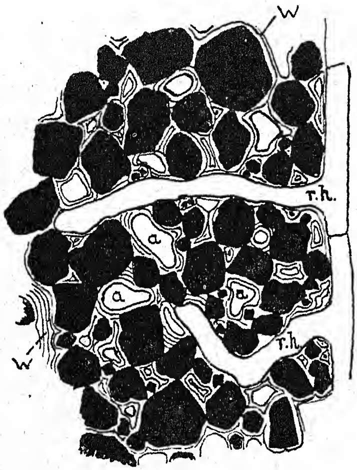

FIG. 340. Diagram of soil with root-hairs (*r.h.*) to show the distribution of air (*a*) and water (*w*) (much enlarged). Soil-particles in black.

If it be desired to determine the *water-content* of the soil, 100 grams are placed in a weighed evaporating dish, after which dish and soil are heated over a water-bath for several hours at a temperature slightly below 100° C. After cooling, the whole is reweighed and the heating is continued until the weight is constant. The difference between the first and the final weights represents the water-content in 100 grams of the soil, the result being usually expressed as a percentage of the dry weight.

A process known as *mechanical analysis* serves to estimate the proportions of particles of different sizes. A rough method consists in placing a small quantity of soil in a tall glass cylinder which is then nearly filled with water. Thereupon the contents are thoroughly stirred until the liquid is uniformly turbid, after which the soil is allowed to settle. Very soon the coarser sandy particles begin to collect at the bottom, and these are quickly followed by others of progressively smaller size till finally (after many hours or days) the clayey silt becomes deposited as the uppermost layer, leaving the water clear. In this way a separation of the soil into particles of diverse sizes is obtained, and the approximate amount of each can be determined by measuring the thickness of each layer.

The relative quantities of fine and coarse particles in different types of soil vary considerably. A portion of the soil remains floating at the surface of the water. This consists of dark-looking fragments of organic material, the vegetable nature of which can often be recognised.

The organic content can be roughly determined by strongly heating a weighed portion of the *dried* soil in a crucible over a Bunsen burner for some hours to constant weight. The loss represents the organic material, together with water not driven off at 100° C. and carbon dioxide given off from carbonates.

If a number of soils from various localities be examined in the above manner, it will be found that they not only differ widely from one another as regards their air, water, and organic contents, but also in the relative proportions of coarse and fine particles. The extremes are sandy gravels with practically nothing but coarse particles (*e.g.* a pebble-beach), and clayey soils and silts composed almost wholly of fine particles; the London basin furnishes good examples of clayey soils, whilst silts are largely alluvial and best seen near estuaries. Between the two extremes there are many intermediate types. Thus, soils consisting of sandy and clayey particles in practically equal amount are known as *loams*. These usually contain little carbonate of lime (*i.e.* are non-calcareous), and many of the plants inhabitating them are described as *calcifuge*, since they are commonly absent from chalky soils. There are, however, clayey soils which contain much calcium (*i.e.* are calcareous), the so-called *marls*, whilst a still larger amount of lime is often present where the subsoil itself consists of chalk or limestone. Species frequenting calcareous soils are described as *calcicole*.

A sandy soil differs from the sandy gravels mentioned above in the smaller average size of its particles, which sometimes compose the entire soil to the exclusion of clay; examples are furnished by the wind-blown sand of dunes and the soil of the Breckland district of Suffolk.

Most soils contain a certain amount of humus which imparts to them their dark colour, and it is this which more or less sharply distinguishes the true soil from the subsoil, *i.e.* the half-decomposed surface of the underlying rock which is in process of being converted into soil. On the exposed face of railway cuttings, etc., soil, subsoil, and underlying rock are often readily recognised (see Fig. 341).

As a general rule no very large amount of organic material is present, although a thin layer of almost pure humus is often found at the surface, but in woodland-soils and garden-mould, for instance, a much larger quantity occurs. Such humus is almost completely disintegrated, chiefly owing to the action of Earthworms, whereas

the *peat* which is found in moorland districts consists of vegetable remains which, owing to the unfavourable conditions for decay, have undergone little change and, moreover, often accumulate to a great depth (see p. 537).

In relation to the plant the important characteristics of a soil are its capability to furnish the necessary mineral salts, its air-content and its power of absorbing and giving up water. Since the water is

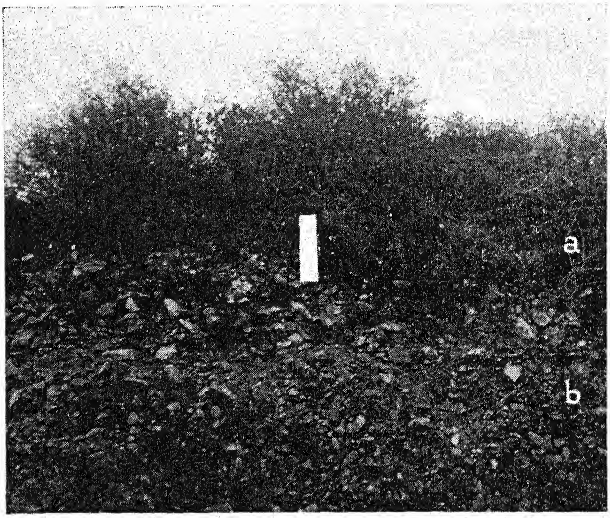

FIG. 341. Photograph to show soil (*a*) and subsoil (*b*). The strip of white paper represents a length of 1 foot. No-man's-land, Hertfordshire. [Photo. E. J. S.]

held as a thin film round each particle, a fine-grained soil, offering as it does a much larger total surface for the water-films than a coarse-grained one, will in an equal volume of soil hold a greater quantity. This can be shown in the following way:—

A number of small holes are drilled in the bottoms and lids of two tins of equal size, after which one is filled with a clayey and the other with a sandy soil, neither being completely dry.[1] The two tins are then placed in a shallow bowl which is filled with water to the depth of about half an inch, and left for an hour during which the water may have to be renewed. Thereupon the tins are removed, the excess of water is allowed to drip off and each is weighed. After that, both tins are heated as described on p. 490 to constant weight. The difference between the first and final weighings will show that

[1] Since moisture passes only very slowly into completely dry soils.

the *water-capacity* of the clayey soil is considerably greater than that of the sandy one. It is instructive to compare other soils in the same way.

When water is absorbed by the root-hairs of a plant (p. 193), they exert an attraction on the film around those soil-particles with which they come into close contact, and thus have to overcome the attractive force which holds the film to the surface of the particle. But as the water-film becomes thinner, this retentive power increases, and consequently at a certain stage of dryness the moisture is held by the soil-particles so firmly that the roots cannot absorb it. In a fine-grained soil, owing to the much larger film-surface, this state will be reached when quite a considerable amount of water still remains, whereas in a coarse-grained soil with its smaller surface the amount of moisture left when the films have thinned out to this limit will be relatively small. There is therefore both water which is *available* and water which is *non-available*, the latter being that which is left in the soil and which can be driven off by heating after plants growing in it show signs of wilting. Whilst a fine-grained soil still containing 12 per cent. of water may already be dry so far as the plant is concerned, a coarse-grained one with 5 per cent. of water would still probably provide sufficient moisture. But the amount of non-available water varies with the external conditions, particularly the rate of water-loss from the plant, and to a much smaller degree with the type of plant concerned.

The action of rainfall, combined with chemical change, plays a considerable part in determining soil-structure, tending to bring about a spatial segregation of soil-particles and dissolved salts.

There are two principal sources of the water in the soil: the greater part is derived directly from atmospheric precipitation from above, some of which is absorbed as it slowly trickles through the earth. Part of the moisture, however, may be drawn up by capillarity from the underground water-table if this be near the surface. Different soils vary greatly in the facility with which they permit the water that falls on their surface to pass through them—in other words, their *permeability* differs. Thus, a coarse-grained sandy soil allows water to drain very rapidly through the large spaces between the particles, so that but little is retained; in such a soil, however, the interspaces are usually occupied by air and there is no risk of water-logging, unless the soil be shallow and situated upon some impermeable layer. The greater the percentage of fine-grained particles, the less permeable does the soil become; the water passes through very slowly, tends to accumulate in the interspaces, and consequently in such a soil there is always a danger of inadequate aeration. A clayey soil, for instance, when

once thoroughly wet, comes to be almost impermeable, a property made use of in the puddling of ponds. This is readily shown by the following experiment (Fig. 342).

Two small tins have their bases perforated by a number of fine holes and are then half-filled with closely packed sandy and clayey soils respectively. Both are then suspended over beakers, and an equal volume of water is added to each. In a given space of time far more water runs through the sandy than through the clayey soil (Fig. 342), and indeed the latter may be quite impermeable. It will be realised, therefore, that coarse-grained soils contain little water but are well aerated, while fine-grained soils have plenty of water but tend to be badly aerated, so that a soil with a duly balanced amount of coarse and fine particles (*e.g.* a loam) will give the most satisfactory combination as regards water- and air-content.

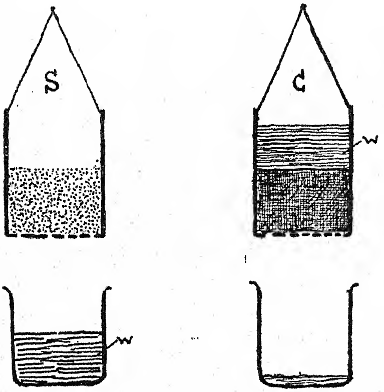

FIG. 342. Experiment to show relative permeability of sand (*S*) and clay (*C*) to water (*w*). The water in the two beakers is shown as it would appear at the end of the experiment.

The permeability of different soils to air can be compared in the following way (Fig. 343): A glass funnel is filled with closely packed wet clayey soil which is prevented from extending into the stem of the funnel by a small pad of cotton-wool. A piece of glass tubing, slightly wider than the stem of the funnel, is fitted at each end with a short length of rubber tubing, one of these being closed with a clip. The glass tube is now filled with water and attached in an air-tight manner by the second piece of rubber tubing to the stem of the funnel. A second similar apparatus is fitted up, employing a wet sandy soil. When the clip closing the base of each tube is opened, water rapidly runs out of the apparatus containing the sandy soil, through which air has passed to take its place, whilst little or none escapes from that containing the clay.

In times of prolonged drought the abundant evaporation from the surface-layers of the soil brings about a kind of suction from below. Inasmuch as the air-spaces form one continuous system, they constitute a series of capillary channels through which the water may rise. The height to which the water can be drawn is, however, not considerable and depends on the small size of these

spaces, and therefore such capillary suction comes into play much more effectively in a fine-grained clayey soil than in a coarse-grained sandy one.

The amount of evaporation of water from the surface of the soil depends on a great many features. In the first place, what has been said above about the strength of attraction between the particles and the water-films has an important bearing on this matter, since in evaporating the water has to overcome this attractive force which, as already explained, increases as the soil becomes drier. The nature of the surface also plays a great part in determining the amount of evaporation. If the surface is kept finely divided (*e.g.* by ploughing, raking, etc.),—in other words, is kept in good tilth,—the uppermost layer of the soil will be dry, but will consist of numerous loose particles with large air-spaces between them. This surface-layer or *mulch* of dry well-aerated earth checks evaporation, inasmuch as the number of fine capillary channels has been greatly diminished; so that, whilst absorption of water by capillary suction goes on as readily as before up to the level of the mulch, the loss from the latter is much less; furthermore, heat-conduction of the surface-layer is greatly reduced so that the soil below is cooler. The interchange of gases between soil and atmosphere is facilitated owing to the larger pore-space and the marked expansion and contraction of the air in the mulch-layer due to temperature changes as between day and night. In many soils natural tillage is effected by the action of Earthworms, Moles, etc.

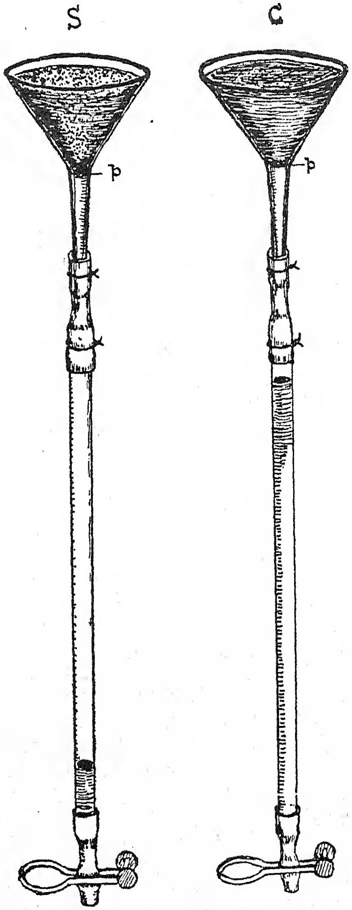

FIG. 343. Experiment to show relative permeability of moist sand (S) and clay (C) to air. p, pad of cotton-wool. The level of the water in the two tubes is shown as it would appear at the end of the experiment.

A surface-crust provides numerous capillary channels for the

upward passage of the evaporating water, besides impeding the ready gaseous exchange between soil and air. An instructive experiment can be performed to illustrate this fact. Two pots are filled with some moist clayey soil and weighed, the surface-layer in the one being kept finely divided, whilst that in the other is pressed down to form a crust. The latter will be found to lose weight much more rapidly than the former. It may be added that in gardens, besides the broken surface of the soil itself, mulches of

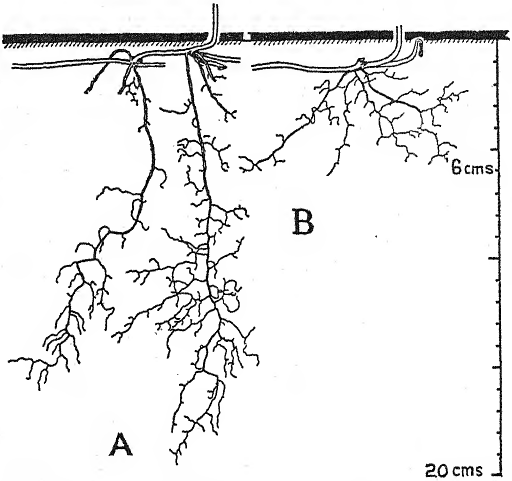

FIG. 344. Root-systems of *Mercurialis perennis* grown in light (A) and heavy soil (B). (After Salisbury.)

straw and dung are often employed. So, too, the soil often remains moist beneath a large stone.

An important physical characteristic of clay soils is that they swell up when wetted and become sticky. This swelling, which is due to their colloidal character, is largely responsible for the impermeability of clayey soils when wet to water and air. As a result, every soil that contains any considerable proportion of minute particles is very hard to dig and is spoken of as *heavy* in contrast to coarse-grained soils, with little cohesion between the particles, which are easy to dig and are termed *light*. The sticky nature of clay is associated with the large proportion of particles of a colloidal size to the surface-action of which this feature is due. The texture of a soil affects materially the extent of the root-system (Fig. 344 and p. 511).

It is possible to modify the characteristics of clayey soils—in other words, to make the heavy soil lighter—in one of several

ways. The simplest (which is, however, difficult to apply on a large scale) is to mix a certain amount of sand thoroughly with the clay. A method extensively employed in this country is to add a top-dressing of lime, for which chalk is often substituted. This has the effect of diminishing the cohesion of the clayey particles and thus of increasing the permeability. Whereas colloidal particles of clay will remain in suspension in a vessel of water for days, the water soon clears if 10 per cent. lime-water or a little acid be added, when the clay becomes flocculated. Humus also helps to lighten a heavy soil, and is occasionally employed in gardens in this way.

The water-retaining power of a sandy soil is sometimes improved by adding clay. The mixing of humus with a sandy soil considerably increases the water-capacity, which at first appears to be anomalous, since humus is used also to lighten soils. The latter application depends on the relatively large size of the humus-particles, whilst their spongy character is responsible for the marked retention of water, a fact which is especially obvious in peat.

The addition of humus to a soil is also of importance to the plant owing to the valuable food-substances which it contains. In fact, a sandy soil without humus furnishes practically no food at all. In clayey soils a good deal more of the nourishment that plants require is present, though not always readily available.

Under natural conditions plants (and animals) die and rot on the soil on which they have lived, and much of the substance which they have taken from the ground returns to it again in the form of humus and other products of decay. In cultivated land, however, this does not apply; a greater or smaller portion of the body of the plant is removed and so year by year the soil becomes more and more impoverished. Hence the necessity, under cultivation, for the frequent application of manures which serve to replenish the stock of mineral food-substances required by the plant for building up its body. The most frequently employed artificial *manures* are nitrogenous (*e.g.* ammonium sulphate), potassic (*e.g.* potassium sulphate), and phosphatic (*e.g.* superphosphate).

Lime is less of a fertiliser than an improver of the soil conditions, both neutralising acidity and altering the texture. Earthworms, in addition to their cultivating action, through the influence of their chalk glands, tend to reduce the acidity of the surface soil in which they chiefly feed. In untilled soils especially, the continued action of rain, charged with carbon dioxide, washes out the soluble salts into the drainage water. It is due to this constant impoverishment, or *leaching*, that the surface soil of old pastures overlying chalk or limestone, for example, may be almost destitute

of calcium salts and even acid in reaction; this leads to a change in the vegetation.

Soil-reaction plays a considerable rôle in influencing plant distribution, very largely in consequence of the concentration of hydrogen ions in the soil-solutions. This not only has a direct influence, but acts indirectly by affecting the solubility of nutrient salts or of toxic substances, such as ions of alumina and iron.

[Important reference-books are: E. J. Russell, *Soil Conditions and Plant-growth*, Longmans, Green & Co., 6th edit., 1932 (636 pp.); S. A. Waksman, *Principles of Soil Microbiology*, Balliere, Tindall & Cox, 2nd edit., 1931 (894 pp.); S. A. Waksman, *Humus*, Balliere, Tindall & Cox, 1936 (494 pp.). For details as to soil structure cf. E. J. Salisbury, "Soil Structure in relation to Vegetation," *Science Progress*, pp. 409–425, 1935.]

CHAPTER XLI

STRUCTURE IN RELATION TO HABITAT

THE fundamental organisation of the plant is essentially the same for that of the desert as for that of the lake or mountain-top, but the detailed structure is nevertheless subject to considerable modifications in harmony with the differing conditions of the environment. The most striking of these modifications are related to the conditions of water-supply in the varied habitats in which vegetation occurs, but light and other factors may also play a part in moulding the structure of the plant. The effect of diverse conditions is most patent when the self-same species occupies two different habitats, as when the same plant grows in both sunny and shady localities or when an aquatic grows on land. Many of the structural peculiarities, associated with environments which necessitate water-economy, are of the nature of *transpiration-checks*, whilst others are connected with the storage of water during times of plenty to be gradually utilised during periods of drought. Among the former the most important are: development of a thick cuticle, depression of the stomata below the general surface (cf. p. 152), restriction of the latter to grooves or pits, copious production of hairs (p. 158), and reduction of the leaf-surface.

Plants with broad thin blades, generally characterised by the absence of transpiration-checks, are commonly termed *mesophytes* (*e.g.* Lime, *Circæa*). Their most marked characteristic is that they wilt when loss of water is comparatively small; hence they are not suited to arid conditions. By contrast so-called *xerophytes*, which often exhibit marked transpiration-checks, can endure pronounced water-loss without wilting, and, if wilted, can recover from a considerable degree of desiccation. Despite the restriction due to the possession of transpiration-checks, xerophytes frequently transpire as rapidly as many mesophytes. The external features, such as small, often scale-like foliage-leaves, cushion-like habit, extreme hairiness, succulence, etc., which tend to retard transpiration, are sometimes spoken of as *xeromorphic characters*.

Most deciduous trees and shrubs have mesophytic foliage, but

by shedding this at the end of the season become xeromorphic, since the whole exposed surface is covered with cork. Perennial herbs exhibit an analogous winter-change through the dying down of the aerial shoots in the autumn (cf. p. 13).

The simplest method of economising the water-supply is perhaps thickening of the cuticle, sometimes supplemented by secretion of wax. The unspecialised annual or perennial herb usually grows under conditions in which the slight variations in the amount of water furnished by the soil are sufficiently compensated by changes in the suction exerted by the plant (p. 193). The leaves are thin and flexible and have a thin cuticle, so that some slight evaporation takes place all over their surface; as compared with the transpiration through the stomata, however, this *cuticular transpiration* is generally quite negligible, except in immature leaves where the cuticle is not yet fully formed. The more strongly the cuticle is developed, the more leathery the texture of the leaf and the less the cuticular transpiration. Such plants are often evergreen and able to retain their foliage throughout the winter, when absorption by the roots is often very slow (cf. p. 13). Plants possessing leaves with a thick cuticle (*e.g. Vaccinium*; Sea Holly, *Eryngium*) can thrive in drier situations because the period during which they remain turgid is prolonged.

Plants which grow in a variety of situations show considerable differences in the thickness of the cuticle. Thus, the leaves of the Bracken or Bilberry (*Vaccinium*) growing on an open heath are thick and leathery, whilst those of the same species growing in the moist atmosphere of a wood are thin and flexible. The efficacy of cuticle thickness in restricting transpiration can be demonstrated by the cobalt method. Leaves with stomata confined to the lower surface are employed, and stomatal transpiration is prevented by means of vaseline.

Dense coverings of hairs increase the thickness of the non-turbulent layer of air in contact with the leaf-surface and check rise of temperature of the leaf (cf. p. 158). The maintenance of a layer of damp air above the stomatal surface is an important aid in checking transpiration, and this can be accentuated in other ways than by the development of a hairy covering. Thus, in many xeromorphic leaves the stomata are depressed below the general surface so that a column of damp air accumulates above each. In the Holly (Fig. 345, A), for example, the stoma is situated at the base of a pit (the *vestibule*) which is formed mainly as a result of the great thickening of the cuticle around the pore. Similar protected stomata occur on the stem-spines of the Gorse (Fig. 345, B), where the cuticle is also very thick.

Plants of damp situations offer a marked contrast in these respects, the cuticle being relatively thin and the stomata often slightly raised above the general surface (Fig. 345, C, D).[1]

Retarded transpiration in wind is also very effectively attained by *restriction of the stomata to grooves or hollows* whose communication with the exterior is often partially occluded by an outgrowth of hairs. A good example is furnished by the common Oleander (*Nerium oleander*). If the lower surface of a leaf be examined with a lens, a large number of light-coloured patches appear dotted

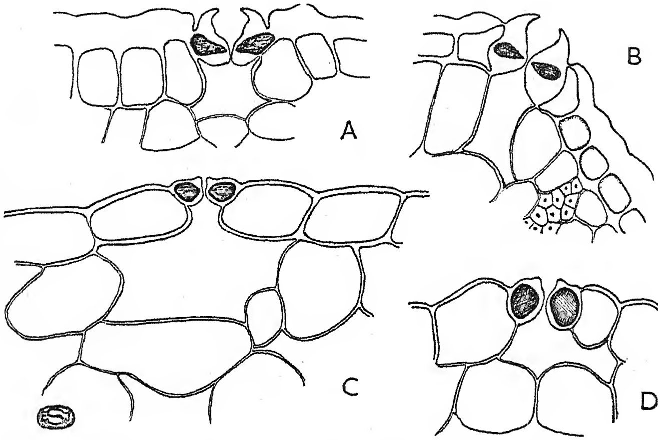

FIG. 345. Stomata. A, Holly (*Ilex aquifolium*). B, Gorse (*Ulex europæus*). C, Brooklime (*Veronica beccabunga*). D, Yellow Pimpernel (*Lysimachia nemorum*).

between the principal veins, each patch being due to a tuft of hairs arising from one of the numerous hollows. In transverse sections (Fig. 346) the latter are seen to extend inwards for slightly more than one-third the thickness of the leaf. The stomata (*St.*) are confined to the portions of the epidermis within these depressions, and interspersed among them are numerous thick-walled unicellular hairs. Each stoma is raised, on a papilla-like ring of cells, above the level of the epidermis lining the hollows, a fact which is not surprising when it is realised that, since the depressions contain a damp atmosphere, the stomata within them develop under the same conditions as those of ordinary leaves growing in moist situations. Other striking features of the Oleander-leaf, apart from the thick cuticle on the exposed surface, are the extremely

[1] Plugging of the stomatal apertures with particles of wax is observed in some plants (*e.g.* certain Conifers), which thereby impede the escape of water-vapour and consequently check transpiration, which is almost entirely cuticular.

lacunar spongy tissue, and the presence of two layers of water-storing hypoderm.

In the Heather (*Calluna*, Fig. 347, A, B) the stomata are confined to a groove (*stomatal chamber*, *st.*) situated on the under-surface of the leaf. The upper or outer surface is protected by a thick cuticle, and the aperture of the groove is closed by interlacing

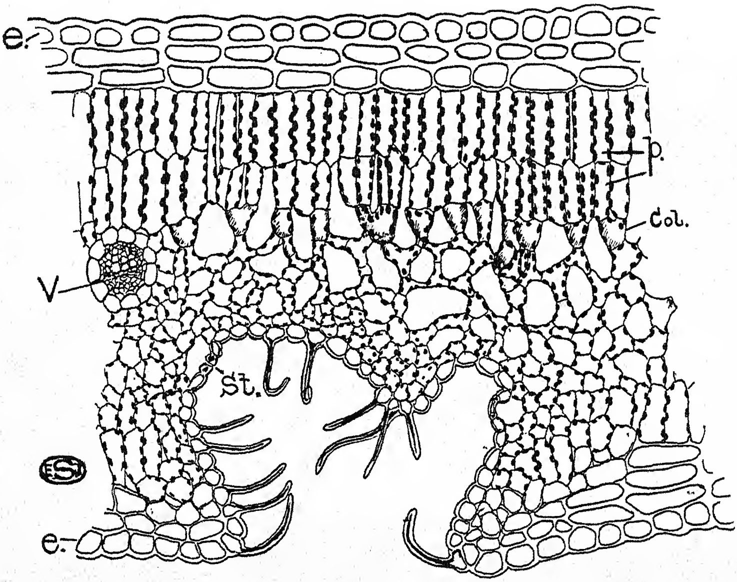

FIG. 346. Transverse section of part of the leaf of the Oleander (*Nerium oleander*) showing a stomatal chamber. *Col.*, collecting cells; *e.*, epidermis; *p.*, palisade layers; *St.*, stoma; *V*, vascular bundle.

hairs (Fig. 347, B). The form of the transverse section is roughly that of an inverted triangle, with the groove occupying a small area in the lower angle and surrounded by the very lacunar mesophyll. The *rolled leaves* of the Crowberry (*Empetrum*) have a similar organisation, except that the stomatal chamber (*st.*) is much larger (Fig. 347, D). More extreme types are found in Grasses (Fig. 347, C), where, moreover, the leaf is often capable of rolling and unrolling in response to changes in humidity (cf. p. 562).

The massing of the foliage in dense rosettes (seen in the Thrift, many Saxifrages, and very commonly in alpine plants) brings the transpiring surfaces into close contact, so that semi-saturated air accumulates in the spaces between them; moreover, such plants are usually of low growth, only sending up a vertical axis in the

flowering season, and are therefore relatively little exposed to wind-currents.

The advantage of such massing together of the transpiring surfaces is well illustrated by trees growing in exposed situations. New shoots that arise on the side of the crown sheltered from the prevailing winds develop normally, but those on the exposed windward side are cut off owing to excessive transpiration. In this and in other ways growth becomes more or less restricted to the leeward side, so that the familiar asymmetrical crown results (Fig. 348).

The deciduous plant meets the conditions of drought in winter by shedding its leaves—that is to say, the transpiring surface becomes greatly reduced. A reduction of surface is, however, exhibited by many plants throughout the year. The foliage-leaves are sometimes of small size, though still carrying on photosynthesis, as for instance in Conifers and *Lycopodium* (Fig. 261, A). A feature which often accompanies such reduced leaf-surface is the absence of markedly dorsiventral structure. In its extreme form this results in the leaf acquiring centric organisation (p. 169).

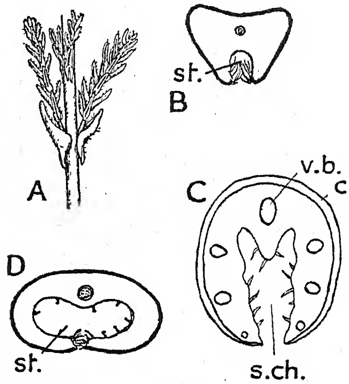

FIG. 347. Reduction of the transpiring surface in xerophytes (A, slightly reduced; the others magnified). A, Small portion of plant of *Calluna*. B, Cross-section of leaf of same. C, Cross-section of rolled leaf of *Festuca*. D, Cross-section of leaf of *Empetrum*. *c.*, cuticle; *s.ch.*, chamber containing damp air; *st.*, stomatal chamber; *v.b.* vascular strands.

A good example is furnished by *Hakea*, a native of Australia, in which the leaves are pinnately branched, the cylindrical segments being slightly flattened on the upper surface. A transverse section of a pinna shows the customary thick cuticle and deeply sunk stomata. Beneath the epidermis are two layers of palisade cells which completely encircle the central parenchyma containing three prominent vascular bundles. Extending between the epidermis and this central region are occasional mechanical elements having thick whitish walls and slightly dilated ends, which probably retard collapse of the palisade tissue during periods of drought. The vascular bundles are accompanied, both on their upper and lower sides, by strands of sclerenchyma. The central region in which the bundles are embedded consists of colourless water-storing (aqueous) tissue in which are scattered occasional large tannin-

cells having deep brown contents. A comparable type of centric leaf is seen in *Pinus* (cf. p. 416).

In the so-called *switch-plants* the leaves are often reduced to mere scales, more or less destitute of chlorophyll, their functions being transferred to the stem. The presence of chloroplasts in the outer cells of young stems (cf. p. 145) has already been noted; but, where the leaf-surface is small, the stem may retain its photosynthetic powers for some years after the inception of secondary

FIG. 348. Wind-trimmed trees at Criccieth, North Wales. Note that the crowns of the trees are almost at right angles to the trunks. [Photo. E. J. S.]

thickening, and may even become enlarged by wing-like outgrowths whereby its efficiency is increased. The Broom (*Cytisus scoparius*), the Whortleberry (*Vaccinium myrtillus*, Fig. 349), the Rush (*Juncus*), and *Equisetum* (p. 386) furnish examples of such *photosynthetic stems*. In the first-named downward prolongations from the margins of the leaf-bases give the stem a ridged appearance. A cross-section shows the usual thick-walled epidermis beneath which, in each ridge, there is a strand of fibres; but, except for these, the whole periphery of the cortex consists of a layer of palisade tissue succeeded by four or five layers of closely packed cells, also containing chloroplasts. The stomata occur at intervals throughout the parts of the epidermis overlying the photosynthetic tissue. In other respects the stem exhibits the normal structure of a secondarily thickened axis.

The leaves of the Whortleberry, though not greatly reduced, are usually deciduous, so that during the winter the plant carries on

photosynthesis only by means of its winged stem. Beneath the epidermis is a continuous zone of photosynthetic tissue (Fig. 349, *as.*),

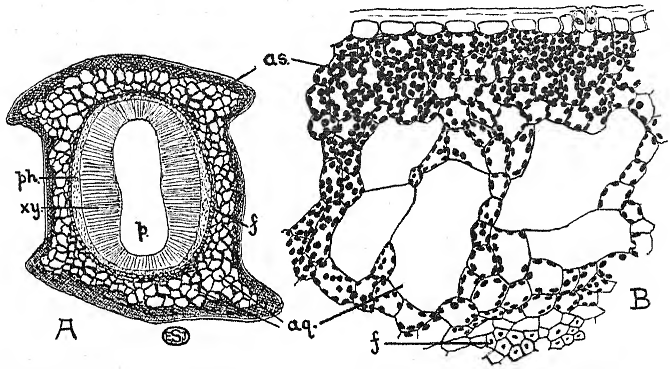

FIG. 349. Diagram of transverse section (A), and detail of small portion (B), of the green stem of the Whortleberry (*Vaccinium myrtillus*). *aq.*, aqueous tissue; *as.*, photosynthetic tissue; *f.*, fibres; *p.*, pith; *ph.*, phloem; *xy.*, xylem.

consisting of rounded or polygonal cells, uninterrupted by fibres. The inner cortex is formed by a network of chlorophyll-containing

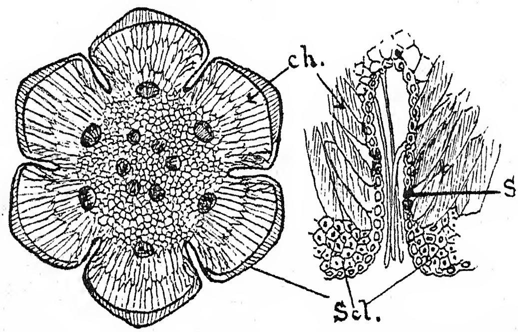

FIG. 350. Transverse section of a young green stem of the She-Oak (*Casuarina*) with the stomatal grooves; one of the latter is shown enlarged on the right. *ch.*, photosynthetic tissue; *S.*, stoma; *Scl.*, sclerenchyma.

cells in which the meshes are occupied by large aqueous elements (*aq.*).

In the She-Oaks (*Casuarina*) of Australia, which supply valuable timbers, the leaves are scale-like. The green twigs possess longitudinal grooves (Fig. 350) to which the stomata (*S.*), protected by hairs, are restricted. The stomata are located at the sides of each furrow, and are situated close to the photosynthetic tissue (*ch.*).

An extreme example of a green stem is afforded by species of *Juncus* in which the leaves are reduced to mere brown scales situated, as in *J. striatus*, at the base of the flowering and non-flowering stems. A transverse section across the stem (Fig. 351) presents an epidermis with thick outer walls and a pronounced cuticle. The sunken stomata are distributed at intervals around the whole periphery, but in surface sections are seen to be arranged in approximately longitudinal series. Beneath the epidermis is a

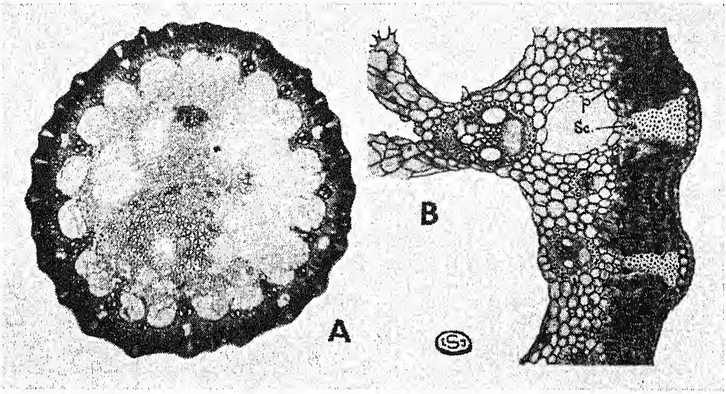

FIG. 351. Transverse section of stem of *Juncus striatus*. A, Complete section under low magnification. The photosynthetic tissue appears as a black peripheral zone interrupted by light patches constituting the mechanical tissue; a ring of over 20 bundles is seen bordering the very large pith composed of stellate cells. B, A small portion on a larger scale, showing one large and three small bundles. *p.*, photosynthetic tissue; *Sc.*, sclerenchyma.

typical palisade tissue interrupted by the large respiratory cavities below the stomata. Within the photosynthetic tissue follows an irregular ring of typical Monocotyledonous bundles accompanied by sclerenchyma. The large pith consists of stellate parenchyma. Rushes afford excellent examples of plants which, though growing in wet places, exhibit a xeromorphic structure. The reason is not yet fully understood.

A peculiar type of xeromorphy is seen in the Butcher's Broom (Fig. 353, B) and *Asparagus* (Fig. 352), where, as in the switch-plants, the leaves are reduced to mere scales, whilst their photosynthetic functions are taken over by specially modified branches known as *cladodes*; such are met with quite commonly in the desert-regions of the earth. In *Asparagus* a tuft of narrow leaf-like branches, on some of which the flowers are borne (in reality a dwarf shoot-system), arises from the axil of each scaly leaf

(Fig. 352, *l*), whilst in the Butcher's Broom the cladodes arise singly and are broad leathery leaf-like structures which, through a twisting of the base, are placed more or less vertically (Fig. 353, B, *cl.*). They are axillary to scale-leaves (*l*) and, on the upper surface of each cladode, there is a small scale-leaf (*s*) in whose axil one or two flowers appear in March or April.

A similar structural modification is seen in many species of *Acacia* where the leaf-blade has become reduced or suppressed, while the vertically expanded petiole or *phyllode* takes its place (Fig. 417).

A cross-section of the cladode of the Butcher's Broom (Fig. 354) shows an epidermis (*ep.*) with thick outer walls, but no appreciable depression of the stomata. The latter (*St.*) are protected by two pairs of ridges which extend around the pore, creating a double vestibule. The upper and lower epidermis are alike, and this, as well as the absence of a marked palisade layer, can be related to the "edge-on" position which this modified branch assumes. The photosynthetic tissue is almost uniformly developed. The central region of the cladode is occupied by large water-storing cells (aqueous tissue, *Aq.*; cf. below p. 510). The arrangement of the vascular tissue is analogous to that of a petiole. Phyllodes have a similar structure to cladodes, and the leaves of many Monocotyledons show an analogous organisation.

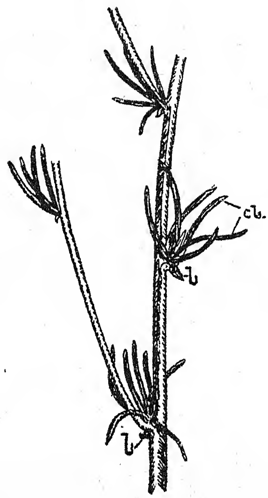

FIG. 352. Small portion of a branch of *Asparagus* with cladodes (natural size). *l*, scale-leaves on main stem; *cl.*, cladodes.

The advantage of a photosynthetic stem-structure over a leaf in conditions of possible water-shortage is mainly due to the resistance to shrinkage offered by mechanical tissue which is more readily formed in branches and petioles than in the lamina itself. There are, however, plants of dry habitats in which copious sclerenchyma is formed in the blade and in which the leaves are highly resistant to conditions of drought.

Leaves or branches often take the form of hard, stiff *spines* which contain vascular tissue and abundant sclerenchyma. A good example is afforded by the Gorse or Furze (Fig. 355, D) where both leaf and branch spines occur. If grown in a moist atmosphere few or no spines are formed and normal flexible foliage-leaves, although of small size, are produced. The seedling

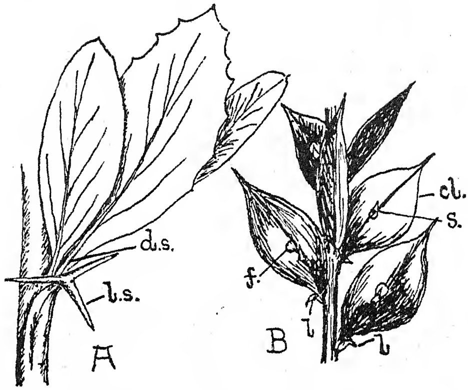

FIG. 353. A, Small portion of branch of Barberry (*Berberis*), showing the three-branched leaf-spines (*l.s.*) (natural size); the foliage-leaves arise from a dwarf-shoot (*d.s.*) in the axil of the spine. B, Branch of Butcher's Broom (*Ruscus*) with cladodes (natural size). *cl.*, cladode; *f.*, flower; *l.*, scale-leaves on main stem; *s.*, ditto on cladodes.

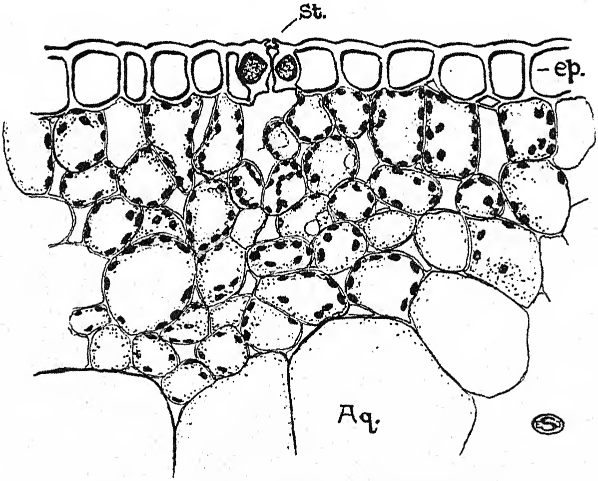

FIG. 354. Transverse section through part of a cladode of the Butcher's Broom (*Ruscus aculeatus*), showing a single stoma (*St.*), the thick-walled epidermis (*ep.*), and the aqueous tissue (*Aq.*) below the photosynthetic zone. The chloroplasts are shown black.

of the Gorse (Fig. 356), moreover, does not immediately bear spines, these only appearing when the shoot has grown to some height above the surface of the ground; this may be related to the fact that the air immediately above the soil is relatively moist, as compared with that at higher levels.

Instances of *leaf-spines* are furnished by the Barberry (Fig. 353, A, *l.s.*), where the leaves on the long shoots are replaced by three-branched spines, in whose axils arise dwarf-shoots (*d.s.*) bearing ordinary foliage-leaves and inflorescences. In the Gooseberry

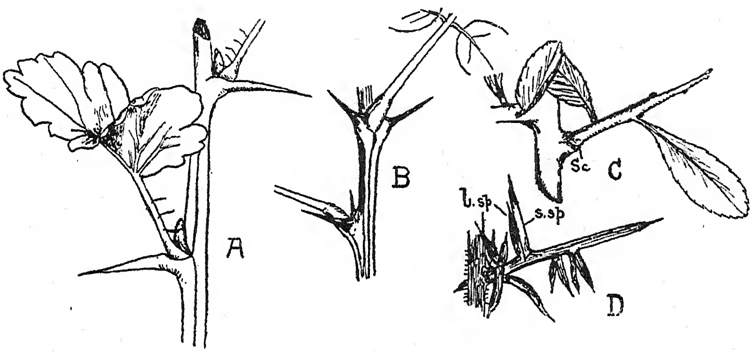

FIG. 355. Examples of spinous plants (all figures natural size). A, Gooseberry (*Ribes grossularia*) (leaf-spines). B, False Acacia (*Robinia*) (stipular spines). C, Sloe (*Prunus spinosa*) (stem-spines). *sc.*, leaf-scar. D, Gorse (*Ulex*) (leaf- and stem-spines). *l.sp.*, leaf-spine; *s.sp.*, stem-spine.

(Fig. 355, A) the spines, which are simple or branched, can be recognised on the summer-shoots as outgrowths from the leaf-base, whilst in the False Acacia (Fig. 355, B) they arise in pairs at the base of the petiole and are modified stipules.

Stem-spines are seen in the Sloe (Fig. 355, C), the Hawthorn, etc., and are recognised not only by their axillary position, but also by the fact that they often bear leaves. Many xeromorphic plants have leaves with spiny margins, as in the Holly, Thistles, etc.

Spines are no doubt in most, if not in all, instances an expression of the tendency to increase woody tissue under conditions of reduced water-supply, but when they occur they may often be of value to the plant in keeping off browsing animals.

Apart from the development of transpiration-checks there is a second method of providing against shortage of water, often found in combination with the first. Thus, many xerophytes store up water in aqueous tissue and, when this represents a large part of the plant, the latter acquires a succulent character.

The Stonecrops and Houseleeks (Fig. 357) afford good examples

of leaf-succulents, whilst stem-succulents are well illustrated by Cacti, in which the leaves themselves are represented by spines. Such succulents can exist for a very prolonged period without external supply of water, during which they gradually shrivel more and more. Owing to their very thick cuticles they transpire very slowly and hence the moisture stored up within them lasts for a long time. Most of these forms have become so suited to dry conditions that their roots rot in a soil of average dampness.

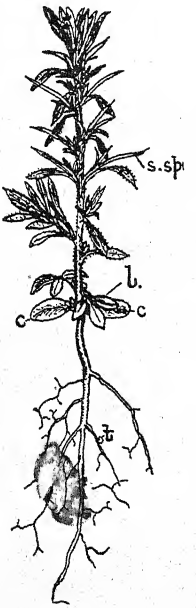

FIG. 356. Seedling of *Ulex*, showing transition to spines (natural size). *c*, cotyledons; *l*, first foliage-leaves; *s.sp.*, stem-spines; *t*, root-nodule.

Aqueous tissue, already observed in the Butcher's Broom (Fig. 354, *Aq.*) and *Hakea*, is a most prominent feature of succulents. In the leaves of the Stonecrop (*Sedum*), the Prickly Saltwort (*Salsola kali*), and the Sea-blite (*Suæda*), the large colourless and thin-walled cells in which water is stored up form the bulk of the leaf-tissue. The aqueous tissue occupies the centre of the leaf, with the photosynthetic tissue towards the periphery; in *Salsola* these tissues are sharply marked off from one another (cf. also Fig. 90, A, p. 150), but in the other two there is a gradual transition between them. Similar water-storing tissue is encountered in stem-succulents (e.g. *Cactus*). Through the loss of water, by transpiration and absorption by the adjacent green cells during periods of drought, the cells of the aqueous tissue shrink, and this results in the walls becoming thrown into small folds which disappear, during the wet season, as the plant regains turgidity. Loss of water from such aqueous tissue is often retarded by the presence of thin mucilage in the cell-contents which exudes from a broken surface as a slimy fluid (e.g. *Mesembryanthemum*).

A certain amount of protection from excessive transpiration in strong sunlight is obtained in a few plants by the leaf-blades assuming a more or less vertical position (e.g. *Iris*). The advantage of the upright position lies in the fact that the incident rays are oblique, and therefore in great part reflected; thus, their heating effect is much diminished. This is seen in the so-called "Compass-plants" (e.g. *Lactuca scariola*). In a shady situation their leaves are spread out in the usual horizontal position, whilst in a sunny

locality the blades are vertical with the edges facing north and south, so that the edge is always presented to the sun at the hottest part of the day. The leaflets of the Wood Sorrel are often found, on a hot summer's day, more or less drooping as in the night-position (cf. p. 268 and Fig. 173), whilst those of the False Acacia (*Robinia*) under these circumstances become tilted upwards at an acute angle; this is a position opposite to that assumed at night, when the leaflets droop downwards.

The modifications of the shoot discussed in the preceding pages all serve to harmonise the plant with its surroundings; so that a

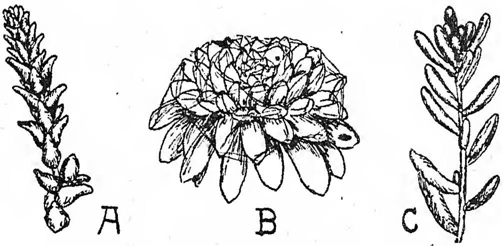

FIG. 357. Examples of leaf-succulents (all natural size). A, Yellow Stonecrop (*Sedum acre*). B, Houseleek (*Sempervivum arachnoideum*). C, White Stonecrop (*Sedum album*).

comparison of different kinds of plants growing under similar conditions, even in widely separated regions of the earth's surface, often reveals a similar physiognomy. But, even in the individual itself mesophytic and xeromorphic features may be united (*e.g.* deciduous trees), bearing a definite relation to changing circumstances. So, too, the seedling does not necessarily resemble the adult (cf. the Gorse). Finally it should be added that, though some of the modifications cited vary with the conditions of growth, others are more or less fixed and tend to put a limit to the variety of circumstances under which the plants possessing them can thrive.

The fact that xeromorphic features are sometimes found in plants of damp habitats, as for instance in the succulent *Sedum pilosum* which grows in bogs (cf. also *Juncus*, p. 506), is probably indicative of the limitations due to heredity. On the other hand many plants are extremely plastic, particularly with respect to leaf-structure (pp. 521, 551).

Variation in root-growth should not be overlooked. In some species this growth is rather uniform, whilst in others the mode of development and extent of the root-system is profoundly modified by competition and especially by the density of the soil, as can be demonstrated by growing the same species in a root-observation box (p. 106) in a light sand or in a heavy clay (Fig. 344).

CHAPTER XLII

THE ECOLOGY OF WOODLANDS

THE study of the social life of plants [1] can be begun by a consideration of woodlands, because this type of vegetation has a designation which is at once used in popular parlance and further coincides with a botanical conception. All woods are characterised by trees as the most conspicuous feature of their vegetation. Beneath these there are usually shrubs or smaller trees (Fig. 360), forming an *undergrowth* which is more or less dense according to the type of wood, and, on the ground, a growth of herbaceous plants (the *ground-flora*, Figs. 359 and 361).

With marked differences in soil-characters are associated differences in the tree-layer so that woodlands of diverse types can be distinguished. Thus, on non-calcareous soils (cf. p. 491) one generally finds woods of Oak (*Quercus*) or Birch (*Betula*), whilst calcareous soils frequently bear woods of Beech (*Fagus*) and Ash (*Fraxinus*). Where there are intermediate types of soils the woodlands may show a mixed character (*e.g.* the Oak-Ash woods found commonly on marls). Hand in hand with differences in the dominant [2] tree, the kind as well as amount of undergrowth and ground-flora will be found to change. But whilst the component species may vary to such an extent that two woods have few kinds of trees, shrubs, or herbs in common, yet those found in the first are replaced by similar physiognomic types in the second, bearing the same relation to one another. Such a definite kind of vegetation as deciduous woodland can be recognised as a major type of *plant-community* in which the leafless period is associated with unfavourable climatic conditions. The different types are characterised by the prevalence of different trees (Oak, Ash, etc.) and associated shrubs and herbs.

[1] A simple description of most of the commoner British communities is to be found in H. Drabble, *Plant Ecology*, Ed. Arnold, 1937 (142 pp.). For details, see the work of C. Raunkiaer, cited on p. 487.

[2] A dominant is a species which by its height and area plays a predominant part in determining the biotic conditions. When there is a single dominant we speak of a *consociation*; where more than one plant shares the dominance, the community is termed an *association*.

The woodland is therefore a plant-community having a definite structure with three tiers, viz. the trees, the undergrowth, and the ground-flora. The important factor light is the one which most markedly limits or restricts the kinds of plants that can persist in the undergrowth and ground flora. This is due to the production of a more or less dense canopy of foliage, either by the uppermost tier of trees or the second tier of shrubs, and as a consequence the character of the flora of a woodland depends largely on the amount of shade cast by the constituent members. In the deciduous woodland, however, we must distinguish between the "*light-phase*" during the winter months, when trees and shrubs are devoid of leaves, and the "*shade-phase*" from about May to November, when the canopy of foliage cuts off a large proportion of the light.

The light-intensity requisite for the growth of a particular species must be one at which the rate of gain by photosynthesis exceeds the loss due to respiration. The intensity at which these processes balance is the *compensation point* (p. 240) and its value varies with the species concerned.

The conditions in each stratum of the woodland differ in respect to humidity, light-intensity, the supply of carbon dioxide, and other factors. Hence within the woodland community itself, we can distinguish what may be termed *partial habitats* and such can often be recognised in other types of vegetation.

LIGHT-INTENSITIES IN WOODLANDS AS PERCENTAGES OF THAT IN THE OPEN (After Salisbury).

Woodland Type.	Light-phase (Winter). Per cent.	Shade-phase (Summer). Per cent.	Ground-flora.
Beechwood (*Fagetum*) .	17–40	0·4–21	Scanty or 0.
Oakwood (*Quercetum roburis*).	19–61	0·2–17	Vernal.
Oakwood (*Quercetum sessiliforæ*).	33–90	0·9–27	Vernal and æstival.
Birchwood (*Betuletum*) .	40–63	18–57	Æstival.

Of our woodland trees the Beech, found on chalky soils in the south-east of England, usually casts the deepest shade both in the light- and shade-phases, owing to its extensive branching and perfect leaf-mosaic (p 122). Furthermore, the "packing" of the relatively flat Beech leaves when wet probably checks gaseous exchange between air and soil. Hence the conditions of aeration are poor, whilst the shallow, richly branched roots of the Beech trees tend to render the surface-soil dry. A striking feature of such a wood is the paucity of vegetation upon the ground and the

almost entire absence, except at the edge, of shrubby undergrowth (Fig. 358). The species, as well as the individuals, of the ground-flora are few, but, wherever there is a clearing (Fig. 359) or the trees are sparsely scattered, the abrupt increase of vegetation shows at once that the soil is not at fault.

The commonest herb of the Beech-wood consociation is the Dog's Mercury (*Mercurialis*, Fig. 359), and it is significant that

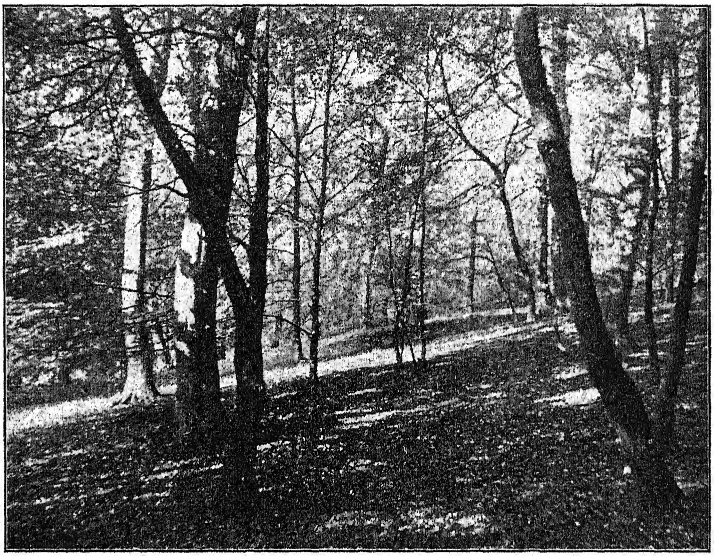

FIG. 358. Interior of a Beech-wood, Pitstone Hill, near Tring, Herts. Note the absence of undergrowth. [Photo. E. J. S.]

this is one of the earliest of our native plants to form new leaves. Other frequent species, sometimes abundant in the better-lighted parts, are *Sanicula* (Fig. 359), the Woodruff (*Asperula*), the Wild Strawberry (*Fragaria*), and the Enchanter's Nightshade (*Circæa*). The first three retain part of their foliage during the light-phase and so are able to carry on photosynthesis during the winter months, whenever the temperature permits. A certain number of Orchids are usually found in Beech-woods, the most characteristic being the large White Helleborine (Fig. 359), whilst the saprophytes *Neottia* (Fig. 132) and *Monotropa* (Ericaceæ) are often met with in the height of the summer, even in the densest parts of the wood, since they can flourish in deep shade. In the autumn their place is taken by numerous Fungi which grow in the humus formed by the fallen leaves. The Yew and White Beam (*Sorbus*

aria) are characteristic associates of the Beech. Where, as at the edge of the wood, undergrowth develops, the most frequent shrubs are the Hawthorn, *Viburnum lantana*, *Cornus sanguinea*, *Euonymus europæus*, and *Acer campestris*, while climbers are represented by *Tamus* and *Clematis*.

In marked contrast to the Beech-woods, but occurring on similar calcareous soils, particularly limestones, are consociations

FIG. 359. Ground-flora of a clearing in the Beech-wood shown above. The vegetation consists chiefly of *Sanicula*, with *Mercurialis* in the foreground; on the right are two leaves of the Wood Burdock (*Arctium nemorosum*); just to the left of these is a plant of the White Helleborine (*Cephalanthera pallens*), bearing three flowers. [Photo. E. J. S.]

of the Ash (*Fraxinus excelsior*) (Fig. 360). This tree casts very little shade and comes into leaf late in the season; in correspondence with this there is usually a varied and abundant undergrowth and ground-flora, though the extreme development of the shrub-layer may itself lead to the production of so dense a canopy as almost to prevent the growth of herbs beneath.

A frequent associate of the Ash is the Wych Elm (*Ulmus montana*), and the commoner shrubs include the Hawthorn, Hazel, Maple, Privet, *Viburnum lantana*, and other species common also in scrub on calcareous soils. *Mercurialis perennis* is often abundant, whilst among the characteristic species of the herb-layer are the Solomon's Seal and Herb Paris (*Paris quadrifolia*). Where, as in

the flushes, the soil is damper, *Allium ursinum*, *Colchicum autumnale*, and *Adoxa moschatellina* are often common.

Since Oak-woods are very common in many parts of England, they may be considered in greater detail. The amount of shade cast by the Oak is more or less intermediate between that cast by the Beech and Ash. Two species of Oak are found in Britain, each of which forms woods on appropriate soils. The most

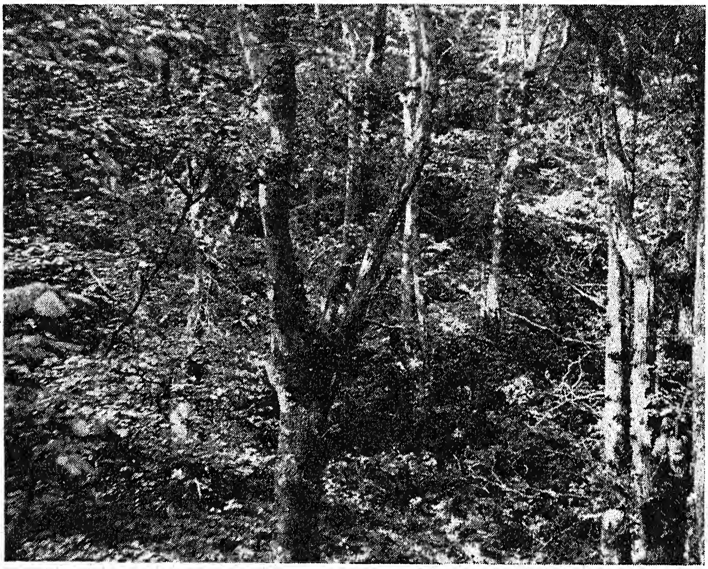

FIG. 360. Interior of an Ash-wood, Clifton Woods, Bristol. The dense shrubby undergrowth is seen below, whilst in the fork of the tree in the foreground a plant of *Polypodium* occurs as an epiphyte. [Photo. E. J. S.]

frequent species, and that usually planted, is the Pedunculate Oak (*Quercus robur*) in which the leaves are often glabrous on both surfaces and the lamina ends somewhat abruptly, at its point of insertion upon the often short petiole, in a pair of lobes with the margins slightly turned over (Fig. 362, A). The other species, the Sessile-fruited Oak (*Quercus sessiliflora*), bears star-shaped hairs on the under sides of its leaves and the blade tapers towards its insertion on the relatively long petiole (Fig. 362, B).

Quercus robur forms woods chiefly upon deep and heavy soils, such as clays and clayey loams which are well supplied with nutrient salts, and the community to which it gives rise may be termed the *Pedunculate Oak-wood* (Fig. 361). Other trees besides

the Oak are frequently found and of these the commonest are

FIG. 361. Ground-flora of a Pedunculate Oak-wood in early spring. The vegetation consists chiefly of *Scilla* and *Mercurialis*. In the background are seen the stems of Hazel and Hornbeam forming the undergrowth. [Photo. E. J. S.]

usually the Wild Cherry, Birch, Maple (*Acer campestris*), Ash (*Fraxinus*), Holly (*Ilex*), and sometimes the Crab. In certain localities the Hornbeam (*Carpinus*) is a prominent feature, though when it occurs it is frequently coppiced (*i.e.* cut down periodically) and then forms the main feature of the undergrowth (*e.g.* on the less calcareous clays of North London). The Hornbeam which has a leaf-mosaic like that of the Beech (cf. Fig. 71), forms a much denser canopy and the result is a ground-flora poor in number of species and much resembling that of a Beech-wood. As a general rule, however, the shrub-layer consists mainly of Hazel (*Corylus*), amongst which commonly occur bushes of Hawthorn, Sloe, Dogwood, Willows, Roses, and Brambles, as well as the Honeysuckle (*Lonicera*).

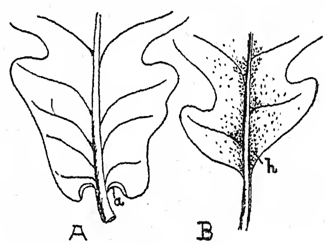

FIG. 362. Portion of leaf of A, *Quercus robur*, and B, *Q. sessiliflora* (about two-thirds natural size). *a*, basal lobe showing margin turned over. *h*, hairs.

The most frequent members of the ground-flora in such a wood, often forming large expanses (Figs. 361, 363), are the Wild Hyacinth (*Scilla*, Fig. 363), Primrose, Lesser Celandine (*Ficaria*), Wood Anemone, Yellow Deadnettle (*Galeobdolon*), Dog's Mercury (Fig. 363), and in less abundance various kinds of Dog-violet. Of great frequency, but not forming such pronounced sheets, are a large number of species, the more familiar of which are the Bugle (*Ajuga*), *Ranunculus auricomus*, Wood Sorrel (*Oxalis*), Barren

FIG. 363. Ground-flora of a Pedunculate Oak-wood in early spring, showing *Scilla* and *Mercurialis*.

Strawberry (*Potentilla fragariastrum*), Enchanter's Nightshade, Ground Ivy (*Nepeta*), Cuckoo-pint (*Arum*), and several Grasses (Melic, Vernal, False Brome Grass, etc.). In the Oak-woods of Kent the Milkmaid (*Cardamine pratensis*) often covers large areas, whilst on the more loamy soils the Wood Sandwort (*Arenaria trinerva*), Woodruff (*Asperula*), Wood Sanicle (*Sanicula*), Wood Sage (*Teucrium*), Foxglove, and Bracken are conspicuous.

If we follow the story of the wood from the early days of spring to the fall of the year, we are confronted with the problem as to how the soil is able to accommodate and nourish so many individuals and such a constant succession of forms. The solution is in part furnished by the subterranean architecture of the wood, for just as we find the aerial organs forming three definite tiers, each utilising the sunlight that has passed through the layer above, so too in the soil beneath we find a layering of the root-systems.

Those of the trees and shrubs are naturally the deepest, whilst the shallow ones of Grasses and of some of the herbs are nearest the surface. The intervening layers are occupied by many roots, frequently belonging to plants with underground storage-organs, such as the Wild Hyacinth (*Scilla*) and Cuckoo-pint. Owing to this stratification of the root-systems, competition is to some extent diminished as between those occupying different layers, whilst owing to the successive development of the flora the overground shoots mainly compete with those produced in the same season.

Woodland plants probably receive a twofold benefit from their habitat, firstly in the form of shelter and secondly by the absence of sun-loving competitors (cf. p. 486). To any one who possesses a garden it is a familiar observation that the majority of plants in deep shade bloom either very sparsely or, more frequently, not at all, and what is true of the garden-flowers is in general true also of wild species. The early flowering of most woodland plants is to be related to the fact that at this time of the year the overhead canopy has not yet formed. It may be recalled that a higher light-intensity is often necessary for flower-formation than for the development of vegetative organs (p. 247). All the commonest plants found in the interior of woodlands such as the Anemone, Dog's Mercury, Primrose, Wild Hyacinth, and Lesser Celandine have finished blooming, and often have formed their seeds, before the canopy is complete. Not only does the shade prevent the development of the flowers of most plants, but also, where these possess attractive mechanisms for insects, their conspicuousness would be to a great extent lost. It is probably in relation to this that many of the later-flowering woodland plants are highly scented, *e.g.* Woodruff (*Asperula odorata*), Honeysuckle, Butterfly Orchis (*Habenaria chlorantha*), etc. Most of the later-flowering woodland plants are either found where the canopy is more open or at the edge and by the sides, constituting the so-called marginal flora.

No less essential than the development of flowers, however, is the formation of food-material for growth and reproduction. It is therefore of supreme importance to the members of undergrowth and ground-flora that their leaves should be produced early, so that photosynthesis may proceed whilst light is plentiful. In many plants of other habitats the period of maximum growth and subsequent flowering does not take place till after the first-formed leaves have provided the necessary material. But in a woodland the bulk of the growth and flowering is accomplished at the outset, and in relation to this we find that most members of the ground-flora are perennials possessed of some kind of storage-

organ in which food-substances, elaborated during the previous season, are held in readiness to supply the material for growth and reproduction in the following spring. Examples are seen in the bulbs of the Wild Hyacinth, Daffodil (*Narcissus*), and Broad-leaved Garlic (*Allium ursinum*), the corms of the Cuckoo-pint and *Colchicum*, the tuberous roots of the Lesser Celandine, and the fleshy rhizomes of the Wood Anemone, Moschatel (*Adoxa*), and Enchanter's Nightshade (*Circæa*).

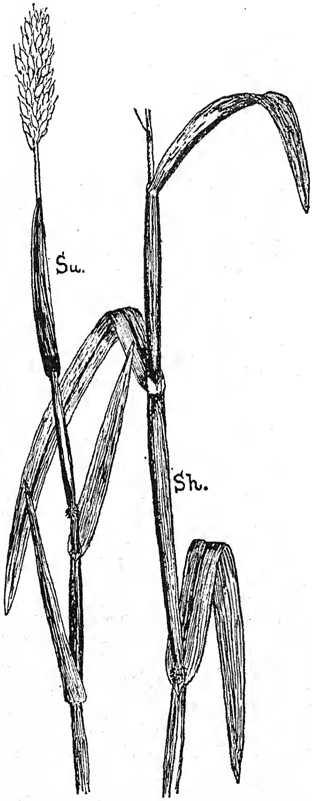

FIG. 364. Sun- (*Su.*) and shade- (*Sh.*) forms of *Holcus mollis* (about two-thirds natural size).

With the advent of the shade-phase the foliage of many species withers (e.g. *Scilla*, *Adoxa*, *Ficaria*, *Anemone*, etc.), but other less pronounced shade-species (e.g. *Ajuga*, *Primula*) retain their foliage throughout the summer, although the rate of photosynthesis is then considerably diminished. The efficiency of the leaves in this respect is, however, to some extent compensated by further growth in area, so that a larger surface is presented to the light. The protection from wind and the heat of the sun, afforded at this stage by the canopy above and the vegetation around, now probably makes this possible, since there is little risk of excessive transpiration. It should, however, be emphasised that the summer-green species are usually found only where the light-intensity during the shade-phase is not very low. Just as many of the herbs form their new leaves before those of the woody plants expand, so too the foliage of the shrubs usually develops before that of the trees above. Each layer thus benefits to some extent by the greater illumination of the "light phase."

The long internodes of many woodland plants (p. 246) leads to a wide separation of the leaves and consequently little mutual shading. Moreover, during development, the blades of such shade-plants take up the position best suited to receive the incident light (cf. p. 122), excellent examples being afforded by the Bracken

and *Holcus mollis*. Both these plants, when growing in bright sunlight, place their leaves at an acute angle with the direction of the sun's rays, thus minimising their effect (Fig. 364, *Su.*); in light

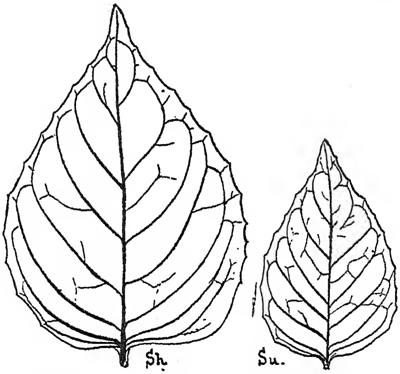

FIG. 365. Sun- (*Su.*) and shade-leaves (*Sh.*) of *Circæa lutetiana* (about one-half natural size).

of medium intensity, however, the blades of the Grass and the pinnæ of the Bracken are arranged so as to receive the light at right angles to the surface, whilst under the deep shade of trees the whole

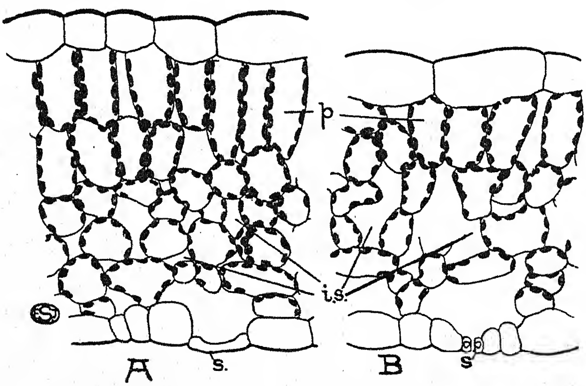

FIG. 366. Transverse sections of the sun- (A) and shade- (B) leaves of the Yellow Deadnettle (*Galeobdolon*), on the same scale. *i.s.*, intercellular spaces; *p.*, palisade tissue; *s.*, stoma (in A, cut longitudinally).

leaf bends over so as to absorb the oblique rays that come in under the canopy of overhead foliage (Fig. 364, *Sh.*).

Plants when growing in the shade exhibit structural adaptation to the changed conditions. In general *shade-leaves* are larger (Fig. 365), thinner (cf. Fig. 366), and very commonly, if the leaf

be lobed or compound, not so deeply cut as the corresponding sun-forms. The colour is usually a fresher green, owing to a high chlorophyll-content, less decomposition of the chlorophyll through absence of strong light, and the greater translucency of the leaf; moreover, chloroplasts are not infrequent in the epidermal cells (*e.g.* Bracken). Production of hairs is usually much reduced in the shade-form (*e.g.* Yellow Deadnettle, Dog's Mercury).

The cuticle and outer epidermal walls of the shade-forms are thinner than in the sun-forms (Fig. 366), a feature which can be related to the greater humidity of the air. A comparison of strips of epidermis from the two kinds of leaves shows that the later walls of the epidermal cells tend to be straighter in the sun-form where the leaves are thicker (cf. p. 150). The palisade cells (*p.*) are shorter and the number of palisade layers, as compared with leaves growing in bright light, may exhibit reduction (*e.g.* Beech), accompanying which there is a relative increase of spongy tissue, whose intercellular spaces (*i.s.*) become much more conspicuous. The last-named feature may perhaps facilitate transpiration in a humid atmosphere. As a general rule the stomata are not depressed in the shade-form, whilst this condition is very common in the sun-form. On the other hand, they are generally more numerous in an equivalent area of the latter, the fewer stomata in the shade-form being related to the larger size attained by the intervening cells. In shade-leaves the vascular tissue is less developed.

When the undergrowth of a wood has been coppiced, the increased access of light finds expression in the much greater vigour and larger amount of the ground-flora, thus showing that light, and not soil-conditions, was the limiting factor. The majority of Oak-Hazel woods are periodically coppiced at more or less regular intervals, so that the herbaceous vegetation waxes and wanes, being least when the undergrowth is thickest, and most abundant about the second or third year after coppicing.

Many herbaceous plants (Pig-nut (*Conopodium*), Yellow Deadnettle, etc.) flower little, if at all, when growing in deep shade, at or near their compensation point, but do so profusely after the wood is coppiced.

Upon loams, sands, shallow siliceous soils, and even on those heavy clays which are likewise poor in mineral salts and often acid in reaction, the characteristic tree is *Quercus sessiliflora*, forming the *Durmast Oak-wood*; the same tree also frequently occurs on the sides of rocky valleys (*e.g.* on the slates of Wales and the sandstones of Yorkshire, Fig. 367), where it may form woods up to 1000–1200 feet altitude. Some of the commonest species of the ground-flora in this community are the Bracken, *Holcus mollis*,

Aira flexuosa, Wood Sage, Whortleberry (*Vaccinium*), Foxglove, Great Woodrush (*Luzula*), Golden Rod (*Solidago*), Hawkweeds, and Ferns. The shrubby layer shows few of the representatives found in the Pedunculate Oak-wood, but Honeysuckle, Brambles, and Holly (*Ilex*) are often common. In the rocky districts above mentioned the ground-flora not infrequently consists almost

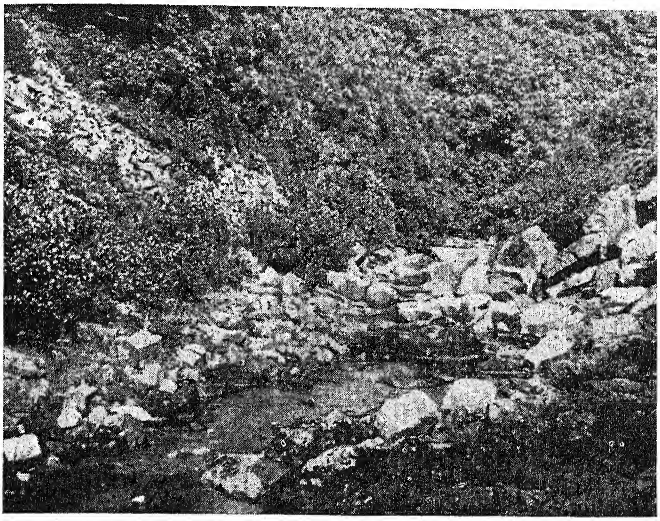

FIG. 367. Durmast Oak-wood, lining the sides of a moorland valley in Yorkshire. On the left, in the foreground and elsewhere at the sides of the stream, are seen bushes of Alder. [Photo. E. J. S.]

exclusively of a carpet of Mosses composed of numerous species (Fig. 368).

On many of the heaths with light sandy soils, *Pinus sylvestris* and Birch (*Betula*) cover extensive areas, frequently occurring intermingled as colonisers, every grade between woods and heath being found. Where the Pine-trees grow close together they form evergreen woods, casting a dense shade, and the ground is usually devoid of vegetation except for a number of Fungi in the latter part of the year. There are also various Mosses, amongst which one known as *Leucobryum* forming grey tussocks is most conspicuous. This Moss shows a structure comparable to that of *Sphagnum* (p. 357), the leaf possessing a single layer of green living cells placed between dead, hyaline, water-retaining elements.

When the Pine-trees are less densely aggregated, a sparse vegetation appears which consists chiefly of Bracken, Whortle-

berry (*Vaccinium*), *Calluna*, *Erica*, Tormentil (*Potentilla erecta*), and occasional Grasses (particularly *Aira flexuosa*), all in varying amounts. The greater the amount of light penetrating to the ground, the more numerous the heath-species that can survive.

Natural Pine-forests are found in Scotland upon morainic soils up to an altitude of 1500 feet.

Natural *Birch-woods* occur above the Oak-woods in mountain

FIG. 368. Interior of a Durmast Oak-wood on slates, Wales, showing the type of ground-flora consisting almost entirely of Mosses. [Photo. E. J. S.]

districts, usually at an altitude of 1000–1200 feet. The dominance of this tree here is an outcome of its great tolerance of exposure. Owing to the efficient dispersal of the wind-borne fruits of the Birch it often colonises felled areas in woodlands on lighter soils. There thus arise semi-natural Birch-woods that are usually replaced in time by other trees that cast a deeper shade, but have a less efficient dispersal. On heavier and damper soils similar colonisation is often effected by the Ash.

By the sides of streams, where the reaction of the soil is usually nearly neutral and the water-content high, woods of Alder (Fig. 367) and Willow frequently occur. The light-intensity in these woods

is low in summer. Ferns and Mosses are common, and many marsh-species, such as *Ulmaria palustris* and *Chrysosplenium oppositifolium* are frequent. In the West of England this is the characteristic home of the Welsh Poppy (*Meconopsis cambrica*).

It should be realised that most soils in our climate, except those which are too shallow or water-logged or which retain too little moisture (*e.g.* pure sand), can support woodlands. Where woodlands do not occur and edaphic conditions like those just mentioned do not obtain, it is usually because there is some factor or factors inhibiting tree-growth. Thus, most grasslands if left untouched would develop into scrub and ultimately woodland. The various phases which the vegetation exhibits until it attains equilibrium with the environment are spoken of collectively as *plant-succession*, and in this country woodlands represent what is termed the *climatic climax*, being the final phase of equilibrium.

CHAPTER XLIII

SEMI-NATURAL COMMUNITIES (SCRUB, GRASSLAND, HEATH, ETC.)

WHEREVER woodlands have been cut down, in the drier parts of the country, their place is taken either by communities of shrubs (scrub) or by heaths, which differ in character according to the soil upon which they grow. Thus, on non-calcareous soils formerly occupied by Oak-wood, we often find a *scrub* notable for the prickly nature of many of the component bushes. So-called commons often bear vegetation of this type, the Gorse being one of the most conspicuous plants. Intermingled with it are numerous scattered bushes of Hawthorn and Sloe, whilst the prickly scrambling stems of Wild Roses and Blackberries are everywhere frequent. Where the shrubby members are less abundant, Grasses, such as the Rye-grass (*Lolium*), Sweet Vernal Grass (*Anthoxanthum*), Dog's-tail (*Cynosurus*), Bent (*Agrostis*), and *Holcus lanatus* are the dominant feature. With these are associated a great variety of herbaceous perennials of which the most frequent are the Buttercups, Clovers, Plantains (*Plantago*), Sorrels (*Rumex*), Cat's-ear (*Hypochœris*), Bird's-foot Trefoil, etc. Along the tracks Plantains, *Polygonum aviculare*, and Rye-grass are a conspicuous feature.

On chalky soils the scrub (Fig. 369) contains, in addition to Hawthorn and Sloe, Spindle-tree (*Euonymus*), Buckthorn (*Rhamnus catharticus*), White Beam (*Sorbus aria*), Elder (*Sambucus*), Wayfaring Tree, Privet, and *Clematis*.

Scrub communities are perhaps the richest in variety of species of all British plant-communities. This may be related to their transitional character. The environmental conditions are not highly specialised and the vegetation is a mixture of meadow-species and of those characteristic of the marginal flora of woods. Most *hedges* are planted, but some represent the last remnants of the broad uncultivated belts of scrub and trees which were left to act as wind-breaks around the cultivated land and which are recalled by the broad haughs of the west country. Hedgerows (cf. Fig. 11, p. 18) in general correspond very closely, both as regards the

constituent shrubs and the accompanying herbs, with the vegetation at the margin of a wood. Just as the latter differs markedly according to the aspect, so too there are striking differences in the vegetation, as well as in the number of species and individuals, on the north and south sides of a hedgerow running from east to west. The flora is both more abundant and varied on the south side. The relationship to woodland is seen in the frequent presence

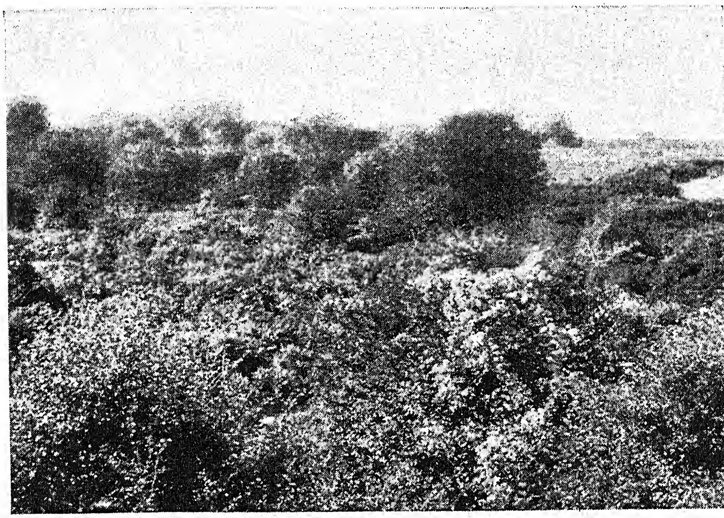

FIG. 369. Chalk-scrub, Berkhamsted Common. The vegetation is mainly composed of Furze, Hawthorn (most of the large bushes in the background), and Sloe. In the foreground, on the right, is a mass of *Clematis* in fruit and, on the left, a bush of *Rhamnus catharticus*. [Photo. E. J. S.]

in ancient hedgerows of such plants as the Primrose, Wood Anemone, and Wild Hyacinth. The commonest shrubs are Hawthorn, Hazel, Sloe, Maple, Dogwood (*Cornus*), and Elder, while on chalky soils the Spindle-tree, Buckthorn, and *Clematis* are often conspicuous. Climbers, both woody and herbaceous, are common. The hedge, moreover, is the special home of the Beaked Parsley (*Anthriscus*), Hogweed (*Heracleum*), Chervil (*Torilis*), Jack-by-the-Hedge (*Sisymbrium alliaria*), and Hedge Woundwort (*Stachys sylvatica*). The frequency of species with succulent fruits, here and at the wood margin, is a feature probably related to the prevalence of birds in both these habitats.

Above the zone of forest on the slopes of our higher mountains there usually follows scrub vegetation which, as the exposure

increases, gives place to *alpine pasture* in which the viviparous *Festuca alpina*, the Mat-grass (*Nardus stricta*), and sometimes the alpine Lady's Mantle (*Alchemilla alpina*) are conspicuous features. But beyond this continuous carpet there follows the vegetation of the rocky summit where, partly owing to lack of soil and partly to exposure (except in the rock-crevices), the plant-growth is discontinuous and characteristically dwarf, including many Mosses and Lichens. Among the species present in the alpine pasture

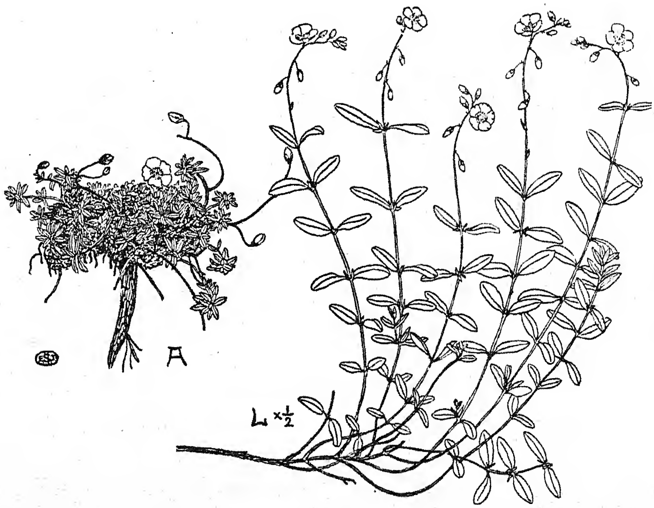

FIG. 370. Alpine (*A.*) and lowland (*L.*) forms of the Rock Rose (*Helianthemum vulgare*). (After Bonnier.)

are many (*e.g.* Dandelion) which also occur at lower levels, and these show differences in habit and leaf-anatomy analogous to those exhibited between sun- and shade-leaves. In this country, owing to the relatively low height of the mountains and the humid atmosphere at their summits, such differences are not well marked. But elsewhere (*e.g.* in the Alps) the leaves are commonly thicker and smaller, and have a better-developed palisade tissue, than those of the corresponding lowland form, though they possess a looser texture owing to the large intercellular spaces. A rosette- or dwarf-habit is very common (cf. Fig. 370); and to this may probably be related the frequent presence of more numerous stomata on the upper, as compared with the under, surfaces of the leaves, since the latter are closely adpressed to the humid soil.

Grassland communities are mostly semi-natural in the sense that they would pass into scrub or woodland but for human or

other interference, though natural grasslands occur on very shallow soil and above the tree-limit on mountains. Of the semi-natural grasslands two main types can be distinguished according to the treatment they undergo, viz. *meadows* which are cut once or twice a year and *pastures* which are constantly browsed. In both types the pruning prevents passage to scrub or woodland, but whereas meadow-land is often characterised by tall associated herbs, pastures are mostly distinguished by the presence of rosette-plants.

FIG. 371. Vegetation of a meadow. The chief plants are Dutch Clover, Buttercups, Daisies, Yellow Rattle, and Grasses. [Photo. E. J. S.]

The vegetation of *meadows* consists typically of a number of robust Grasses, such as the Meadow Foxtail (*Alopecurus pratensis*), Timothy Grass (*Phleum pratense*), the taller Fescues (*Festuca pratensis*), *Poa pratensis*, *Arrhenatherum*, etc. With these are associated a great variety of other perennial herbs, many of which are tall when in flower. Amongst these *Ranunculus acris*, the Sorrel (*Rumex acetosa*), and Dog-daisy (*Chrysanthemum leucanthemum*) are often abundant, whilst other common species are the Yarrow (*Achillea millefolium*) and Clovers. The damper meadows, often spoken of as water-meadows, frequently contain a number of typical marsh-species (p. 538), and others, such as the Meadow Rue (*Thalictrum flavum*), Water Avens (*Geum rivale*), *Geranium pratense*, etc., are conspicuous features.

Owing to the density of meadow vegetation the air near the

ground is very humid and becomes drier as the tops of the Grasses are approached. This feature is reflected in the structure of the leaves of the rosette species, those near the ground being much less hairy than those borne on the flowering stems.

The low-growing *grassland of calcareous soils* (*e.g.* of chalk-downs) has since remote times been the grazing ground for sheep. It is usually dominated by *Festuca rubra*, together with Quaking-grass (*Briza media*), *Bromus erectus*, *Avena pratensis*, *A. pubescens*, etc., which form a close turf. One of the most striking features, however, of this type of pasture is the wealth of blossom in the early summer. The numerous chalk-loving plants which form these floral carpets include the Milkwort (*Polygala*), Purging Flax (*Linum catharticum*), *Anthyllis vulneraria*, Horseshoe-vetch (*Hippocrepis*), Salad Burnet (*Poterium sanguisorba*), Sheep's Scabious (*Scabiosa columbaria*), Dwarf Thistle (*Cnicus acaulis*), *Campanula glomerata*, *Asperula cynanchica*, *Helianthemum*, *Centaurea scabiosa*, *Chlora perfoliata*, *Gentiana amarella*, and Orchids. All of these are of low growth, except when flowering.

The level tops of chalk-downs often exhibit marked leaching of the surface layers of the soil, as a result of which they may be entirely depleted of carbonates, and the calcareous vegetation is replaced by species of acid soils, such as the Heather.

In *pastures* which are not markedly calcareous, species in which the leaves form rosettes close to the surface of the ground are abundant, *e.g.* Daisy, Cat's Ear (*Hypochœris radicata*), *Plantago lanceolata*, and Dandelion. The cricket-pitch or tennis-lawn illustrate in an even more marked degree the effect of repeated artificial restriction of the height of the vegetation. The capacity of the Grasses to compete with and suppress the rosette-herbs is diminished and they tend to multiply at the expense of the turf. Whereas in pastures annuals are usually absent, in close-cut turf bare patches often serve as suitable locations for colonisation by such species as *Sagina procumbens*, *Trifolium filiforme*, etc.

In poor grasslands with thin herbage, where competition is not so severe, there not infrequently occur annuals which are semi-parasitic, such as the Eye-bright (*Euphrasia*), the Red Eye-Bright (*Bartsia*, Fig. 372, A), and the Yellow Rattle (*Rhinanthus*), all of which are parasitic on the roots of the Grasses. These still retain the power of active photosynthesis by means of their green leaves, which, though relatively small, are often larger than those of a true parasite. As a result, many can grow independently of a host, although under these circumstances they are far less vigorous. If one of these plants is carefully dug up with the accompanying soil and the latter gently washed away, the small root-system of the

parasite will be found attached at certain points to the roots of the host (Fig. 372, B and C) by minute disc-like haustoria (*S*). From these, processes penetrate to the vascular tissue of the host and thus absorb nourishment, and in particular augment the water-supply.

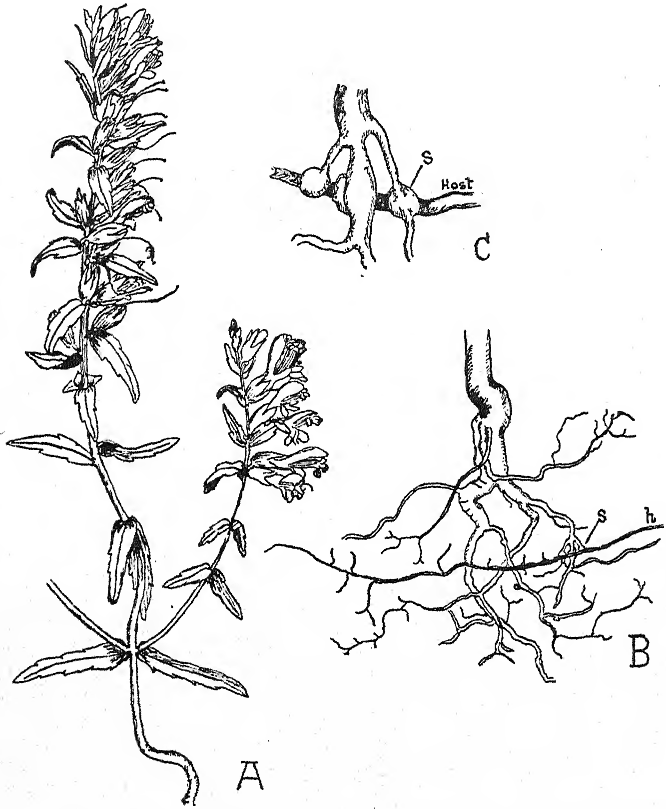

FIG. 372. A, Overground portion of a flowering plant of *Bartsia odontites* (natural size). B, Root-system of the same, showing connection with roots of host (somewhat enlarged). C, A small part of the last (much enlarged). *h*, root of host; *S*, haustorium.

The under sides of the leaves are beset with numerous dome-shaped hydathodes (Fig. 118, B) that act as safety-valves when an excess of water is taken up from the host.

Much of the existing pasture would perhaps pass into scrub and eventually into woodland, but that its condition is artificially maintained by browsing and by fires. The high winds on mountain-tops probably operate in a similar manner. Other causes

contributing to the formation of pasture, both there and elsewhere, are probably the small amount of humus and the dryness of the soil in summer.

The periodical and comparatively frequent disturbance of the soil of *cultivated ground* effectively prevents most perennials from persisting. Indeed, apart from deep-rooted perennials such as Colt's-foot (*Tussilago farfara*), *Equisetum arvense*, Bindweed (*Convolvulus*), etc., the only species which perpetually recur are those which can survive a fallow period, either as seeds or as vegetative fragments. Thus most of the weeds of gardens and arable fields are annuals, such as the Shepherd's Purse, the Groundsel (*Senecio vulgaris*), Fumitory (*Fumaria*), and Charlock (*Brassica sinapis*). Some are winter annuals whose seeds germinate in the autumn (*e.g.* Poppy), others such as the Petty Spurge (*Euphorbia peplis*) and the Scarlet Pimpernel (*Anagallis*) are summer annuals, and these differences in the season of their activity play no small part in determining abundance in relation to particular crops and particular rotations.

The effect of soil is seen in the prevalence of Sheep's Sorrel (*Rumex acetosella*), Knawel (*Scleranthus*), and Field Spurrey (*Spergula arvensis*) on light acid soils, and of Venus's Looking-glass (*Specularia hybrida*), *Galeopsis ladanum*, and Sun Spurge (*Euphorbia helioscopia*) on chalky soils, while the Red Eye-Bright and the Field Mint (*Mentha arvensis*) are a feature of heavy clays. Such perennials as do persist in cultivated soil are chiefly species, like the Creeping Thistle (*Cnicus arvensis*) and the Bindweed, whose rhizomes and roots are not only deep-seated, but fragments of which broken up by cultivation grow out into new individuals.

Heaths (Fig. 374), which are a type of scrub, occur on soils poor in mineral salts (*e.g.* sands and gravels) and acid in reaction, either owing to the nature of the underlying rock or because of the leaching action of high rainfall (p. 497). Heath is characterised by the presence of a usually shallow layer of relatively dry peat containing a considerable proportion of sand. The dominant plant is the Heather or Ling (*Calluna*), sometimes (especially on old heaths) almost pure, or accompanied by the Cross- and Fine-leaved Heaths (*Erica tetralix*, Fig. 373, and *E. cinerea*) and the Whortleberry or Bilberry (*Vaccinium myrtillus*). Occasionally, as in parts of Dorset and Surrey, such heaths become extensively colonised by *Pinus* (cf. p. 523), which eventually kills off the heath-flora.

The typical heath, owing to the deep shade cast by the densely branched *Calluna*, has a relatively scanty flora, sometimes consisting, apart from the dominant plant, almost entirely of Mosses and

Lichens. Where the heath is not so pure the commonest associates of *Calluna*, in addition to *Erica* and *Vaccinium*, are the Dwarf Furze (*Ulex nanus*), Broom, Tormentil, Heath Bedstraw (*Galium saxatile*), Heath Speedwell (*Veronica officinalis*), Woodsage (*Teucrium*), Juniper (*Juniperus*), and Bracken, as well as various Grasses, of which *Aira flexuosa* is the most characteristic. The parasitic *Cuscuta* (p. 214) is also not uncommonly found attacking numerous members of the heath-community.

In the wetter parts of the heath a slightly thicker layer of peat is met with, bearing particularly *Vaccinium* and sometimes *Sphagnum*. The vegetation in such habitats is transitional to that of typical moorland (cf. below).

FIG. 373. Portion of a plant of the Cross-leaved Heath (*Erica tetralix*, natural size).

The soil of a heath is very shallow and generally sandy; moreover, the surface-layer of peat, owing to the large quantity of moisture which it absorbs, largely prevents the access of rain-water to lower levels, so that most of it evaporates again in subsequent warm weather. The peat further absorbs the heat-rays of the sun, so that the surface becomes very warm on a sunny day, a fact which is familiar from the quivering of the air just above the ground at such times. Most heaths finally are exposed and wind-swept. In correspondence with this the characteristic members of the heath-flora are xeromorphic. Moreover, a considerable number of the typical heath-plants are evergreens, for conditions are scarcely more unfavourable in winter than in summer.

The upland *moors* (*e.g.* those of Yorkshire, Fig. 375) are probably to be regarded, like the majority of heaths, mainly as occupying soil formerly dominated by woodland which has been destroyed, either by man or natural agencies. For just as heath replaces woodland in the drier districts, so is moorland found on the site of former forest in those parts where a moderately high rainfall usually obtains. That many of our moors have thus taken the place of woodland can often be seen from the presence of tree-trunks, mostly of Birch, embedded in the peat (Fig. 376). Lowland moors, such as those of the New Forest, on the other hand, appear to have developed from fens (cf. p. 555).

Moors are usually characterised by a soil having a greater depth of peat than heaths and a smaller percentage of intermingled sand, so that the soil has an increased water-retaining

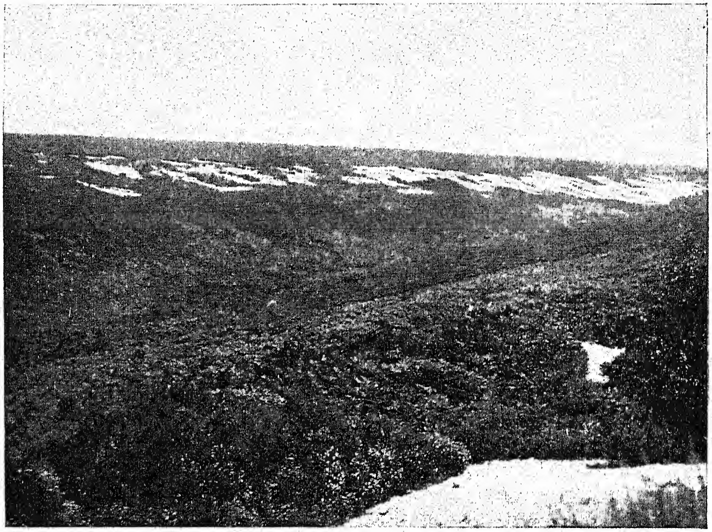

FIG. 374. Heath, Hindhead Common, Surrey. A large proportion of the vegetation on the farther slope consists of *Calluna*. [Photo. F. E. F.]

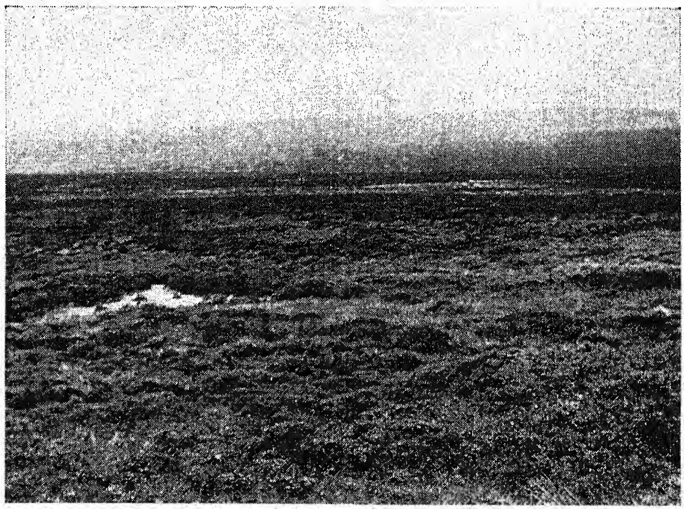

FIG. 375. Distant view of Heather-moors, Yorkshire. The plants in the foreground are mainly *Calluna* and *Vaccinium*, whilst the grassy patch consists chiefly of Cotton-grass and Rushes. [Photo. E. J. S.]

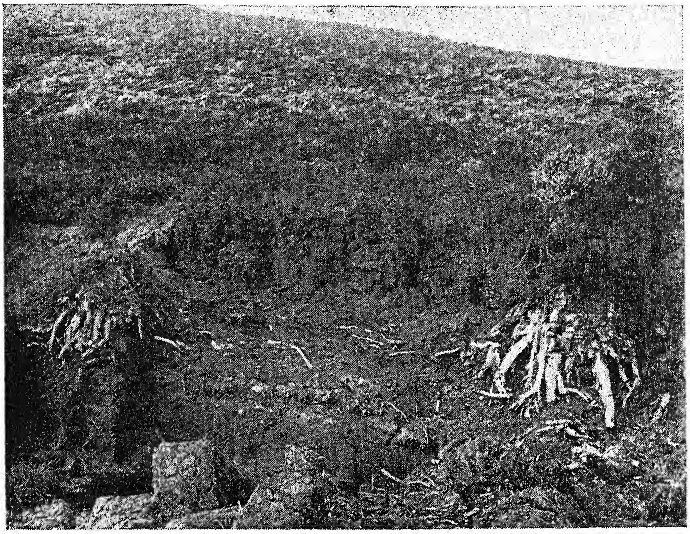

FIG. 376. Section of peat on a Yorkshire moorland, showing embedded trunks of the Birch. The vegetation on the slope above consists of *Calluna* and Bracken. [Photo. E. J. S.]

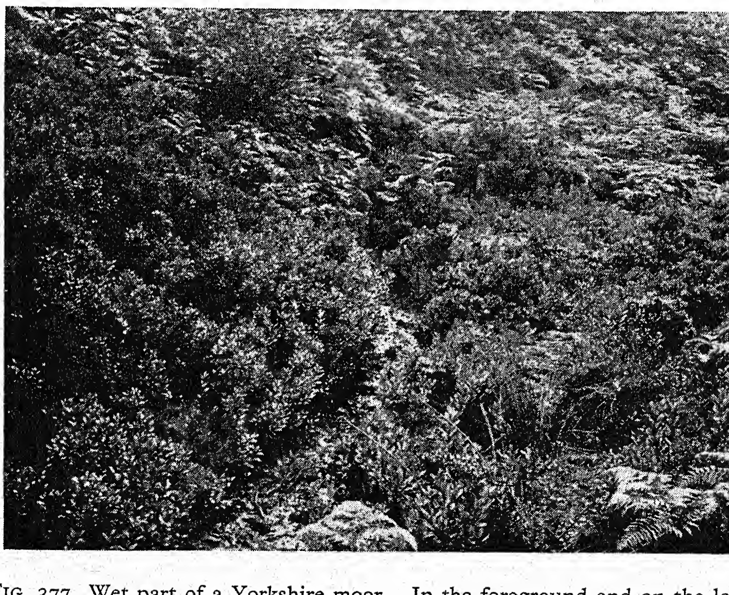

FIG. 377. Wet part of a Yorkshire moor. In the foreground and on the left is a dense growth of Bog-myrtle (*Myrica*), whilst in the background a considerable quantity of Bracken is seen. [Photo. E. J. S.]

capacity. In the wetter parts the peat may attain to considerable thickness, as a result of its rapid formation by such plants as *Sphagnum*, Cotton-grass (*Eriophorum*), etc. Owing to the large amount of acid humus present, the soil-water of the moor is acid in its reaction and thus contrasts very markedly with the often alkaline character of fen-water (cf. p 555).

In the commonest type of moorland, namely, the *heather-moor* (Fig. 375), the dominant plants, amongst which *Calluna*, *Erica*, and *Vaccinium* (all members of the Ericaceæ) are most prominent, all possess xeromorphic foliage, whilst most are devoid of root-hairs, the function of which is taken over by mycorrhiza (cf. p. 218). In view of the soil being relatively wet, the xeromorphic character appears surprising, but the poor aeration owing to its water-logged character, the low temperature of the soil, and the toxicity of the soil-water all tend to lower the rate of absorption by the roots. Moreover, moorlands are usually to be found in more or less exposed wind-swept situations tending to accentuate transpiration. The retentive capacity of the peat for water may also play a part, but this is to a large extent compensated by the heavy rains and mists in the districts where moors occur.

The commonest of the shrubby associates of *Calluna* on such a moor are species of *Erica* (Fig. 373), *Empetrum*, and *Vaccinium*. These together form a vegetation with somewhat low growth and of a more or less even level, so that the plants afford one another mutual protection. The last of these shrubs has deciduous leaves with a thick cuticle and becomes a switch-plant in winter (cf. p 504). Frequent moorland plants are the Blue Moor-grass (*Molinia cœrulea*), the Bog-rush (*Juncus squarrosus*), the Deer Sedge (*Scirpus cæspitosus*), and the Bracken, besides numerous Mosses of which *Polytrichum* is the chief. In the damper parts (Fig. 377) the insectivorous Sundew (Fig. 134) and Butterwort (Fig. 135) flourish, together with Sweet-gale or Bog-myrtle (*Myrica*), Cranberry (*Vaccinium oxycoccus*), Bog Asphodel (*Narthecium*), *Viola palustris*, various Rushes, *Eriophorum*, Sedges (*Carex*), and *Sphagnum*. The Mat-grass (*Nardus stricta*) often forms almost pure communities on eroding edges of the peat.

It is more particularly on the deeper peat that the Whortleberry finds its chief home, here frequently becoming the dominant plant. In some areas, where the peat is still deeper, an extremely wet soil results bearing a community dominated by *Eriophorum vaginatum* (*Cotton-grass moor*). This plant, which forms peat with very great rapidity, has narrow leaves with a very thick cuticle and is thus suited to exposed situations, whilst its rhizomes traversed

by numerous air-canals enable it to grow in a soil that is completely water-logged (cf. p. 544).

The different types of moorland-communities appear to be determined partly by the water-content of the soil and partly by the degree of acidity and the amount of nutrient salts, features that are often related to the rate of peat-formation, to its depth, and to the amount of associated mineral matter. The dry heather-moor is formed on peat relatively rich in mineral substance and either shallow or up to 4 feet in depth. The very wet Cotton-grass moor, on the other hand, is associated with peat very poor in mineral matter, usually very acid, and attaining a depth of from 5 to as much as 30 feet.

Burning of heath and moorland is often resorted to as a means of encouraging new growth for stock or game. Salts are liberated from the burnt plant-tissues which ameliorate the edaphic conditions and thus tend to modify the character of the vegetation. Such areas often exhibit a distinctive growth which persists for a considerable period, *e.g.* the "swiddens" of the Yorkshire moors. Another method of amelioration of acid moorlands is by means of artificial dykes which flush the soil with drainage water containing mineral salts leached out from higher ground. Such flushes, like the "flushes" in acid woodlands, support a vegetation more like that on neutral soils.

CHAPTER XLIV

THE ECOLOGY OF MARSH- AND WATER-FLORAS

IN low-lying meadows we find considerable variation in the depth at which the underground water-table is situated and, where the latter approaches near to the surface, any depression may furnish a *marsh-flora*, such as is found more particularly round the edges of lakes and ponds and by the sides of sluggish streams. In such a marsh the underground organs of the plants are often submerged, but there may, for the greater part of the year, be no free water apparent above the soil. In these situations (Fig. 378) we find typical marsh-plants, the more characteristic being the Marsh Marigold (*Caltha*), Water-mint (*Mentha aquatica*), Ragged Robin (*Lychnis flos-cuculi*), Forget-me-not (*Myosotis palustris*), Milkmaid, Marsh Thistle (*Cnicus palustris*), Marsh Ragwort (*Senecio aquaticus*), Meadow-sweet (*Ulmaria*), Marsh Horsetail (*Equisetum palustre*), Rushes (*Juncus*), Sedges (*Carex*), and Small Valerian (*Valeriana dioica*); if the soil is somewhat peaty, one meets with additional species, such as Lesser Spearwort (*Ranunculus flammula*), Pennywort (*Hydrocotyle*), Lousewort (*Pedicularis palustris*), Water Blinks (*Montia*), Marsh Violet (*Viola palustris*), Devil's-bit Scabious (*Scabiosa succisa*), and Sneezewort (*Achillea ptarmica*).

Further towards the open water we come to a *swamp-flora* (Fig. 380) in which a certain amount of standing water is usually present above the soil-level, the vegetation often showing a more or less marked zonation corresponding to the depth to which the soil is submerged. Typically three such zones are distinguishable. Beginning with the Sedge-zone on the landward side, there follows a belt of Reeds (*Phragmites*), which is again succeeded by a zone of Bulrushes (*Scirpus lacustris*) next the open water. Among the more characteristic plants of the Sedge- and Reed-zones are *Iris pseudacorus*, Flowering Rush (*Butomus*), Bur-reed (*Sparganium*), Water Plantain (*Alisma plantago*), Reed-mace (*Typha*), Spike-rush (*Eleocharis*), Reed Canary-grass (*Phalaris arundinacea*), *Glyceria aquatica*, Great Water Dock (*Rumex hydrolapathum*), Water Drop-

wort (*Œnanthe*), Purple Loosestrife (*Lythrum*), Hemp Agrimony (*Eupatorium*), Gipsywort (*Lycopus*), Brooklime (*Veronica beccabunga*), Bog-bean (*Menyanthes*), and *Equisetum limosum*. In the third zone the only common associate of the Bulrush is the Mare's-tail (*Hippuris*, Fig. 381).

Although the preceding lists roughly indicate the zonation, the individual plants locally show considerable differences in distribution, so that they are not always necessarily found in the

FIG. 378. Marsh-flora. In the foreground are seen various Sedges (*Carex*), with Marsh Marigolds (*Caltha*) and, more particularly in the background, the leaves of the Meadow-sweet (*Ulmaria*). [Photo. E. J. S.]

belt mentioned; thus, some of the marsh-plants are frequently met with in the swamp-flora, and *vice versa*. Moreover, not uncommonly one or other of the zones is absent, their occurrence depending largely on the rapidity with which the floor slopes. A striking feature of the swamp-flora is the prevalent upright habit and the vertical position of the leaves of the constituent plants (Fig. 380), a habit well suited to a vegetation subject to wind-movement.

Marsh-plants frequently show conspicuous hydathodes, most commonly at the leaf-tip, as in *Myosotis palustris* and *Alisma plantago*. In the latter the tissue above the bundle-ends breaks down completely so that the escaping water-vapour passes directly

to the exterior. The underground organs exist in a medium which is deficient in oxygen. This is to some extent counteracted by copious intercellular spaces which are continued also into the aerial parts. Some members of this flora (e.g. *Lythrum salicaria*, *Lycopus europæus*, *Epilobium hirsutum*) develop on their submerged stems and roots a special aerating tissue which appears as a white spongy swelling. This *aerenchyma* is a very lacunar secondary tissue,

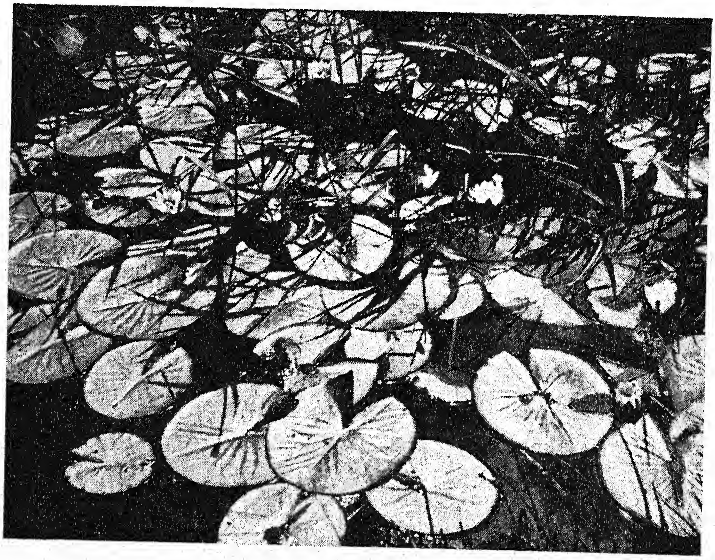

FIG. 379. White Water Lily (*Nymphæa*) growing amongst Reeds (*Phragmites*), Wicken Fen. The floating leaves and flowers of the former are seen. [Photo. E. J. S.]

formed in place of cork by the phellogen, which cuts off cells only on the outside. These remain thin-walled and living and, as they enlarge, partially separate, and so produce a system of wide air-spaces (often concentric in their arrangement) to which the spongy character is due. The function of this tissue is to supply air to the submerged parts, and it is particularly well developed in plants growing in water-logged soil.

As soon as the region with free-standing water is entered *aquatics* begin to appear, so that many of them are found among the members of the swamp-flora (cf. Fig. 379, Fig. 380). Moreover, these aquatics themselves exhibit a zonation, associated with the depth of the water. Near the shore are plants rooted to the bottom and developing floating leaves, but, as the water deepens, the limit

FIG. 380. Swamp-flora, Wisley. The vegetation consists of a thick growth of Water St. John's Wort (*Hypericum elodes*), amongst which is seen the Spike-rush (*Eleocharis*) on the right and *Carex pseudocyperus* on the left. [Photo. E. J. S.]

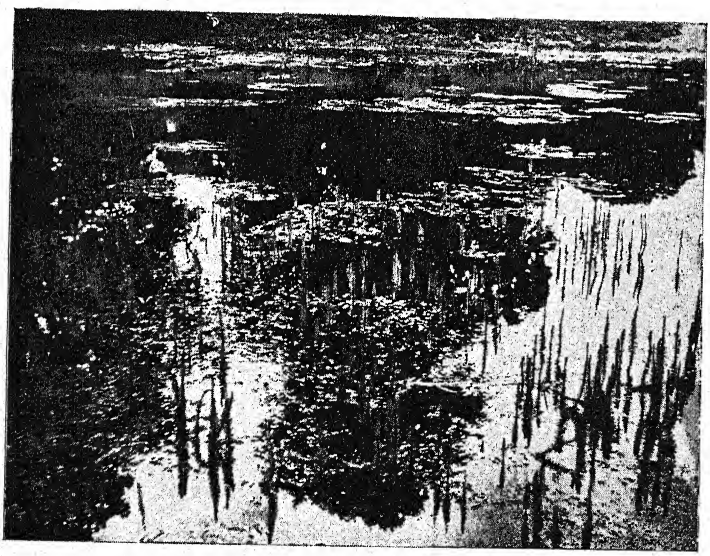

FIG. 381. Aquatic flora, Water-end, Herts. Numerous upright shoots of the Mare's-tail (*Hippuris*) are seen projecting from the water, in which the patches indicate the position of submerged plants of the Hornwort. In the middle the floating rosettes of the Water Starwort

of depth from which they can bring these leaves to the surface is reached and beyond this zone aquatics with floating leaves are absent. Examples are furnished by the White (*Nymphæa*, Fig. 379) and Yellow Water Lilies (*Nuphar*), Water Starworts (*Callitriche*, Fig. 389), Water Crowfoot (*Ranunculus aquatilis*, Fig. 386), Floating Pondweed (*Potamogeton natans*), and *Polygonum amphibium*. In this same zone we get other rooted plants, such as the Arrowhead (*Sagittaria*, Fig. 387) and *Hypericum elodes* (Fig. 380), which raise some of their leaves into the air, and still others, in which only the flowers appear above the water-level, *e.g.* Floating Bur-reed (*Sparganium natans*), Water Violet (*Hottonia*), and Water Milfoil (*Myriophyllum*, Fig. 388), the first two occurring in relatively shallow water. Amongst all these forms are found a number of free-floating aquatics, such as the Duckweed (*Lemna*), Frog-bit (*Hydrocharis*), and Bladderwort (*Utricularia*).

Beyond the belt of floating aquatics which, starting from the shore, extends into considerably deeper water than the Bulrush-zone of the swamp-flora, a number of typical submerged forms can exist at a still greater depth. Such are *Potamogeton lucens*, *Ceratophyllum* (Fig. 382), and *Elodea*. At a still greater depth all aquatic Flowering Plants disappear and we only find the Moss *Fontinalis* and the Stoneworts (*Chara*) and subsequently nothing but Algæ. The latter occur in varying quantity in all parts of the water at certain times of the year, and on rocky shores of lakes, where the marsh-community is not developed, conspicuous growths of *Cladophora*, *Ulothrix*, etc., may be seen.

In streams the rate of flow greatly affects the character of the aquatic flora. Where the current is rapid, free-floating plants are absent and such species as *Sagittaria* and *Œnanthe fluviatilis* grow completely submerged, though they may develop floating leaves in quieter waters. The capacity of water to carry soil particles in suspension depending on its rate of flow, the particles are deposited in proportion as the flow is checked. Under sheltered conditions the deposits tend to consist of varying proportions of fine inorganic and organic silt, whilst where there is constant movement coarse mineral particles will mainly accumulate. Such differences in texture and composition of the bottom deposits have a marked influence on the character of the vegetation. Where the deposit is mainly organic, *Scirpus lacustris* is frequently dominant, whilst when the deposits are richer in mineral salts the Reed-mace (*Typha latifolia*) is often conspicuous.

The submerged parts of all water-plants are surrounded by a medium which is much denser than that enveloping the shoot of a land-plant, so that they receive considerable support. Aquatics

do not therefore require much mechanical tissue. In fact the principal strain to which they are subjected is, as in the roots of terrestrial plants (cf. pp. 6, 109), a longitudinal pull due to currents in the water. Indeed, such mechanical tissue as the aquatic possesses is usually contained in a central strand of vascular tissue (cf. Fig. 382).

Water contains far less oxygen than an equivalent volume of air, so that respiration is attended with considerable difficulty in

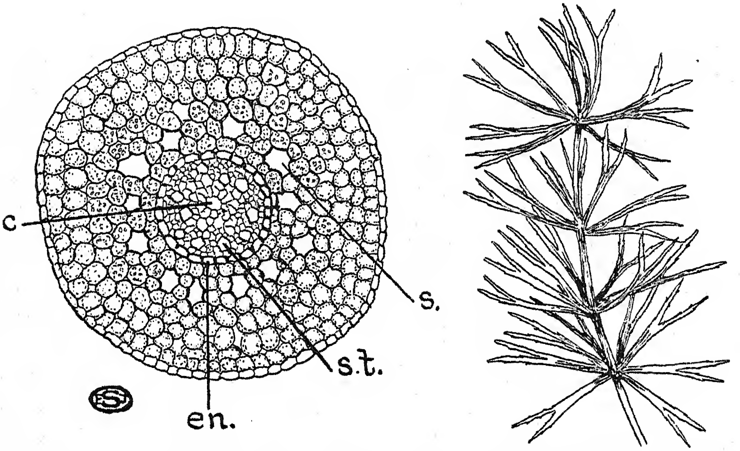

FIG. 382. Habit, and transverse section of the stem, of the Hornwort (*Ceratophyllum demersum*). *c.*, xylem-canal; *en.*, endodermis; *s.*, intercellular space of cortex; *s.t.*, sieve-tube.

aquatics. Carbon dioxide, on the other hand, is more readily dissolved by water and the aquatic consequently has a larger amount at its disposal, bulk for bulk, than a land-plant. Moreover, the supply of carbon dioxide is constantly enriched through the oxidation of organic material in the mud.

The physiological processes carried out by submerged aquatics, whether Flowering Plants or Algæ, may appreciably modify the conditions. Thus, during periods of active photosynthesis there is considerable removal of carbon dioxide, even from bicarbonates, which may lead to the precipitation of carbonates and a decrease in hydrogen-ion concentration. Moreover, oxygen-enrichment may be brought about, especially by the action of Algæ, both attached and free-floating (plankton).

Since there are usually no stomata on the submerged parts of aquatics, both oxygen and carbon dioxide have to enter by diffusion over the whole surface through the very thin cuticle. This is

in itself a slow process. The difficulty in gaseous exchange is compensated by very thin foliage or extreme division of the leaves (Figs. 386, 388), *i.e.* the creation of a large absorptive surface and by the development of a special internal atmosphere occupying the abundant intercellular spaces (Fig. 383).

The relation between anatomical structure and habitat is nowhere more plainly shown than in the *aquatics* among Flowering Plants, which, however, usually betray distinct evidence of their origin from terrestrial ancestors. All the submerged organs of such plants are modified to suit the exceptional conditions of the environment. This is well exemplified by a study of the transverse section of the *stem* of an aquatic like the Hornwort (*Ceratophyllum demersum*, Fig. 382), which grows completely under water. A small intercellular space (*c.*), surrounded by three or four layers of thin-walled parenchyma-cells, occupies the centre of the single vascular strand. This space is actually a longitudinal canal (*xylem-canal*) formed by the breaking down of elements of the procambial strand which, in less extreme aquatics (e.g. *Myriophyllum*), give rise to xylem. Beyond the enveloping parenchyma lies the phloem, which can be recognised by its large sieve-tubes (Fig. 382, *s.t.*). The absence of xylem, whilst the phloem is well represented, can be related to the fact that absorption takes place over the whole surface, whilst conduction of elaborated food-materials remains as necessary as in a terrestrial plant.

The vascular strand is sharply bounded towards the cortex by a well-defined endodermis (Figs. 382 and 384, *en.*), showing suberised thickenings on the radial walls, and immediately within is a pericycle, just as in many young roots. The wide cortex beyond consists of thin-walled parenchyma in which a ring of intercellular spaces (*s.*) surrounds the central strand. These are much larger and often more numerous in other aquatics (cf. Fig. 383). The epidermal cells have thin outer walls with a very thin cuticle, and there are no stomata.

An atmosphere consisting largely of oxygen is produced within the plant during photosynthesis which, owing to the relatively large amount of carbon dioxide, goes on readily; the oxygen formed does not escape into the water, but passes into the numerous large canal-like intercellular spaces of the cortex which traverse all parts of the aquatic (Fig. 383). When it was demonstrated that a water-plant gives off oxygen during photosynthesis (cf. p. 211), the gas collected was escaping from this *internal atmosphere*. The presence of these air-chambers furthermore gives the aquatic considerable buoyancy, and thus helps to maintain rooted forms in an erect position in the water.

The numerous large air-canals of aquatics are often segmented by plate-like septa or *diaphragms* composed of many small cells separated by minute intercellular perforations. These latter are too small to admit of the passage of water, and thus prevent the injection of the air-canals, when fragments of water-plants become detached, as normally occurs in vegetative reproduction; owing to the perforations the flow of air is not obstructed.

Those aquatics, whose lower parts only are submerged, approach more nearly to land-plants in their internal structure. In the Mare's-tail (*Hippuris*, Fig. 384), for instance, the xylem (*Xy.*), which is necessary to supply water to the aerial parts, though not extensive, forms an obvious zone situated within the phloem (*p.*) and surrounding a large central pith (*pi.*). The wide vascular cylinder can be related to the growth of the shoots above the water and the consequent bending strains to which these are exposed. Hence a more peripheral disposition of the mechanical elements than occurs in submerged plants is rendered necessary.

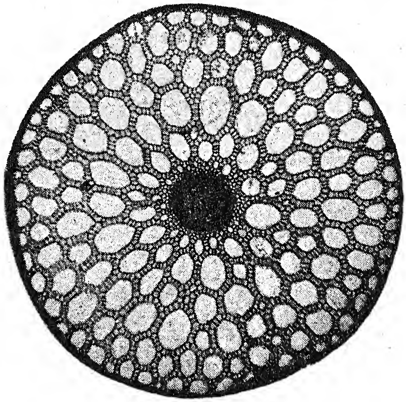

FIG. 383. Transverse section of the stem of *Hippuris*, showing the small central stele and the very wide lacunar cortex.

Even the more extreme aquatics, however, often preserve indications of their terrestrial ancestry in their *vascular system*. Thus spiral vessels commonly persist at the nodes (e.g. *Potamogeton*), and transient spiral vessels occur in the young internodes. In the different species of *Potamogeton* can be found various stages of the concentration and reduction of the vascular system. These features are least pronounced in *P. natans*, which develops a relatively large inflorescence rising some two or three inches out of the water, and further possesses floating leaves. The large central cylinder (Fig. 385) encloses eight to ten fairly well-defined vascular bundles, each of which is separated from its neighbours by two to three layers of thin-walled parenchyma, and consists of a large xylem-canal (*C.*) with accompanying phloem (*P.*). The likewise broad-leaved, but completely submerged, *P. lucens* presents a more marked concentration of the bundles, whose individuality is consequently less pronounced. Lastly, the narrow-leaved *P. pectinatus*, which is also totally submerged, exhibits but

a single xylem-canal surrounded by phloem, as in *Ceratophyllum*. It may be noted that the leaf-traces exhibit a similar reduction, one bundle passing to each leaf in the last-named species, whilst in the two former the trace consists of three bundles. In view

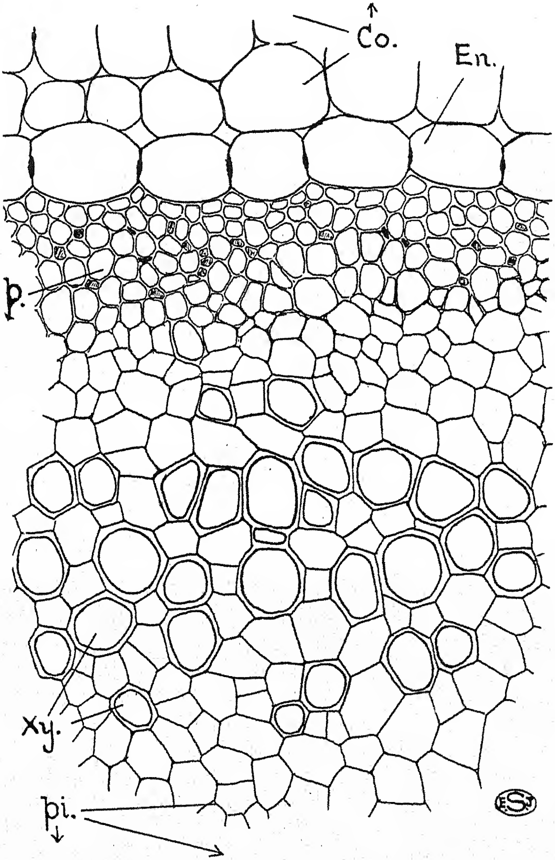

FIG. 384. Portion of transverse section of the stem of the Mare's-tail (*Hippuris*). *Co.*, lacunar cortex; *En.*, endodermis; *p.*, phloem; *pi.*, pith; *Xy.*, xylem.

of the reduction which water-plants show in respect to the vascular tissue, it is scarcely surprising that they rarely exhibit cambial activity. A trace of cambium can, however, be detected in the stem of the Mare's-tail (*Hippuris vulgaris*).

Another condition, which life in water involves, is the reduced illumination to which submerged aquatics are exposed, due to

much of the obliquely incident light being reflected from the surface, whilst that which penetrates is rapidly absorbed as it passes to deeper and deeper levels. For this reason, it is imperative

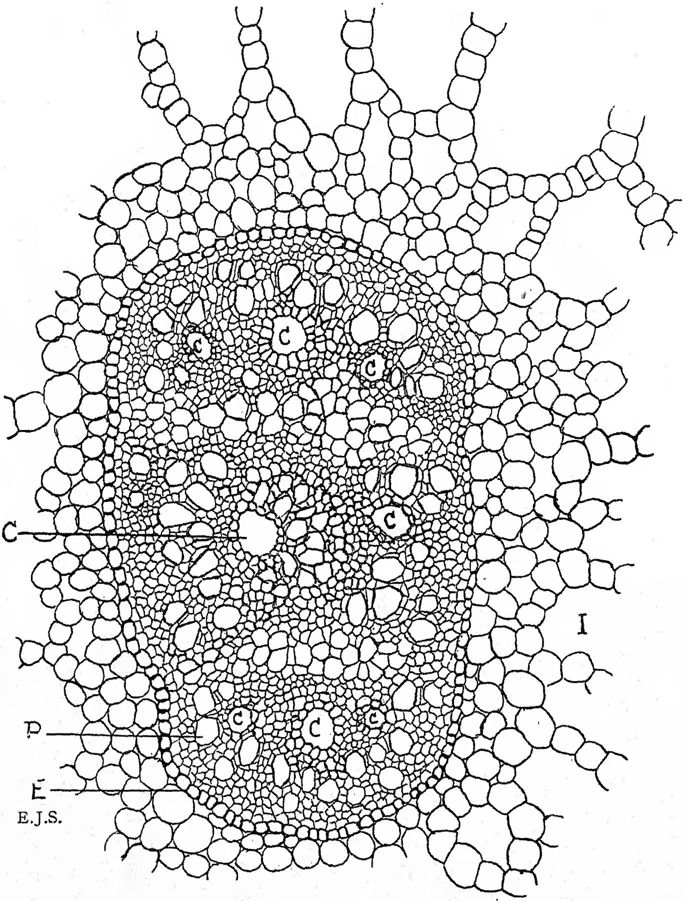

FIG. 385. Transverse section of the vascular strand of the Floating Pondweed (*Potamogeton natans*). *C.*, xylem-canals; *E.*, endodermis; *I.*, air-canal; *P.*, sieve-tube.

for most water-plants to bring their photosynthetic organs relatively near to the surface, and their compensation point largely determines the depth at which submerged aquatics can grow. Naturally the depth to which light penetrates varies with the cloudiness of the water.

The *submerged leaves* of water-plants are either very thin or deeply divided, as in *Myriophyllum* (Fig. 388) and *Ranunculus aquatilis* (Fig. 386). Such division not only affords a larger surface for the absorption of carbon dioxide, but is also mechanically efficient, since currents flow readily between the segments of the leaves. The long undivided leaves of *Potamogeton pectinatus*, which readily trail out with the current, are equally well adapted to offer but slight resistance. Occasionally submerged leaves have a broader surface, as in *Potamogeton lucens* and *Nuphar* where, however, the leaves are very thin and flexible.

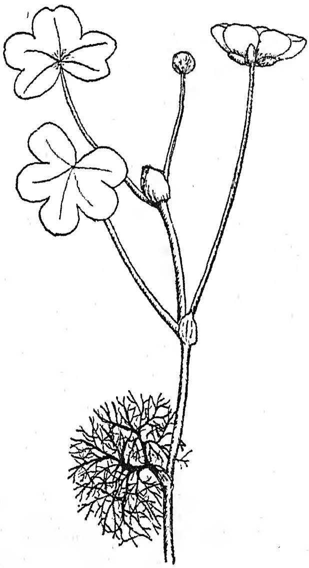

FIG. 386. Portion of a plant of *Ranunculus aquatilis* (about two-thirds natural size), showing floating and submerged leaves.

Aquatics which produce floating leaves as a rule also have a varying number of submerged ones; the latter are generally quite different from the floating leaves, the most notable exception being *Nuphar*, where they are similar in form but very much thinner. The difference is well illustrated by *Ranunculus aquatilis* (Fig. 386), in which the submerged leaves are much divided and feathery, whilst those floating at the surface are reniform. In *Nymphæa* the few submerged leaves are generally ribbon-shaped, whilst the floating ones are deeply cordate with a roughly oval lamina (Fig. 379). A particularly interesting example is afforded by *Sagittaria* (Fig. 387). In still shallow water, three kinds of leaves are produced: firstly, ribbon-shaped submerged ones (Fig. 387, A); secondly, lanceolate or cordate floating ones, often with a deeply notched base (Fig. 387, B); and thirdly, sagittate aerial leaves (Fig. 387, C) standing out of the water; in running (cf. p. 542) or very deep water, however, only the submerged type of leaf is produced.

Floating leaves (Figs. 379, 386, 387, B) agree in mostly having an entire edge and in the fact that the petiole is attached more or less near the centre of the glabrous blade (cf. especially Fig. 379), so that the pull of the leaf-stalk acts centrally and the lamina is kept flat on the surface of the water. The floating leaves of the Water Lilies arise from a stout perennating rhizome; they have

very long petioles, whereby the blade is maintained at the surface, even in relatively deep water, and enough play is permitted for currents to carry it to and fro without submergence.

In *Potamogeton natans* and *Polygonum amphibium*, on the

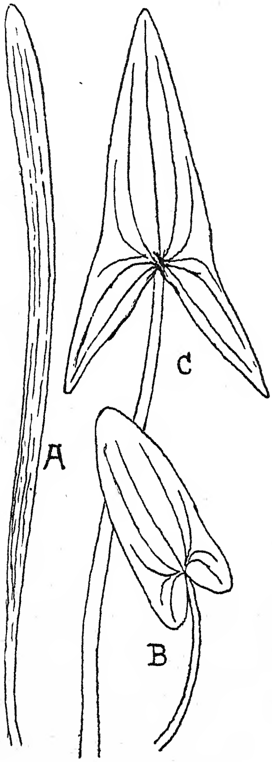

FIG. 387. Different types of leaves of the Arrowhead (*Sagittaria*) (considerably reduced). A, submerged. B, floating. C, aerial.

FIG. 388. Portion of a plant of the Water Milfoil (*Myriophyllum*), showing the inflorescence (consisting of four female flowers at the base and male flowers above) supported by the parachute-like arrangement of the whorled leaves (about natural size).

other hand, the petioles are short, the blades being brought to the surface by the elongation of the stem. In these two plants the floating leaves are separated by much shorter internodes than the submerged leaves, a fact which is more particularly apparent in the Water Starwort (*Callitriche*). Here the opposite leaves on the submerged part of the stem are borne at widely separated nodes, but at the water-surface the internodes are scarcely developed, the leaves being crowded together to form the familiar floating rosettes

(Fig. 389, *W*). The longer internodes of the more deeply submerged portions of the stem in these plants are probably to be related to the reduced light-intensity, a feature which may also be responsible in part for the thin texture of the submerged foliage in many aquatics.

An important function of many floating leaves is that of forming a supporting platform around the base of the aerial inflorescence (cf. Fig. 386). The same function is fulfilled in some plants having only submerged foliage by a parachute-like arrangement of the whorled leaves just beneath the water-level (e.g. *Hottonia*, *Myriophyllum*, Fig. 388).

The leaves of submerged water-plants usually bear no stomata, whilst in floating leaves they are restricted to the upper surface, and exhibit marked differences from the ordinary type. The guard-cells, in transverse section, are roughly triangular through the inner walls being bevelled off towards the outer edge of the pore, where the thickening is most pronounced. By means of their stomata floating leaves maintain a connection between the air-spaces of the submerged portions and the outside atmosphere. As the upper surface of such floating leaves is usually covered by a fine waxy bloom (e.g. *Nymphæa*), this side of the leaf is not readily wetted, and hence the formation of water-films across the stomatal apertures is prevented.

Submerged leaves are generally very simple in structure and, when dissected, are usually centric, as is well illustrated by the leaf of *Ranunculus aquatilis* (Fig. 391, *W*). This centric structure may be related to the absence of illumination from any particular direction, owing to the diffuse character of the light and the constant displacement of the segments by water-currents. Intercellular spaces, as in the stem, are usually abundant. Non-dissected types of leaf, as already noted, are often very thin and may consist between the veins of only two layers of cells (e.g. *Elodea*). Chloroplasts are invariably present in the epidermis (cf. p. 148).

The roots of water-plants are generally all adventitious, forming white slender little-branched structures functioning mainly as organs of attachment, since absorption of water and mineral salts takes place over the whole surface. Some aquatics are rootless, as in *Ceratophyllum* and the Bladderwort (*Utricularia*). In the free-floating *Lemna* and Frog-bit (*Hydrocharis*) the roots hang down into the water, and not only absorb, but also serve to keep the plant balanced in the normal position.

There are comparatively few Flowering Plants that grow in the sea. Amongst the commonest are the Eel-grass (*Zostera*) found in shallow water and *Ruppia* which grows in brackish ditches. The former has long, thin, grass-like leaves.

Aquatics display a remarkable plasticity of structure, particularly in relation to their anatomy, as a result of which many (e.g. *Callitriche*, *Ranunculus aquatilis*) can grow either completely submerged, or on mud, or even on dry land. A comparison of such *land-* and *water-forms*, belonging to the same species, clearly shows the adaptational significance of most of the characters of aquatics. In the *land-forms* the internodes become extremely short, so that the whole plant appears stunted (cf. Fig. 389, *L*); further, the leaves are thicker and smaller (Fig. 389, *L*) and, when divided, show broader and fewer segments, whilst roots are more strongly developed. In *Polygonum amphibium* the land- and water-forms are strikingly different. The leaves of the former are lanceolate and covered with bristly hairs, whilst the floating leaves of the aquatic form are cordate and quite glabrous.

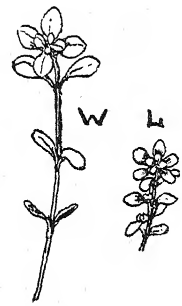

FIG. 389. Land-form (*L*) and Water-form (*W*) of the Water Starwort (*Callitriche*) (natural size).

It is noteworthy that the submerged leaves correspond closely to the juvenile foliage of the same species growing on land, whilst the adult leaves, even of completely submerged aquatics, sometimes approach those of their land-form. In general, conditions which promote increased photosynthesis appear to favour the development of the terrestrial type of foliage.

In a cross-section of the stem of the land-form of *Callitriche* (Fig. 390, *a*) the cortex consists of closely packed rounded cells with small intercellular spaces between them, whilst that of the water-form (Fig. 390, *d*) is mainly occupied by two large air-canals separated only by narrow strips of tissue. Thicker outer walls and a distinct cuticle characterise the epidermal cells of the land-form (cf. Fig. 390, *b* and *e*). The vascular strand of the latter has an almost continuous ring of xylem (Fig. 390, *c*) in contrast to the one or two xylem elements bordering the central canal (*la.*) in the water-form, whose vascular strand is slightly smaller (Fig. 390, *f*). Similar differences are exhibited by the structure of the stems of the two forms in other aquatics.

The leaves of the Starwort do not differ markedly in the two forms, but there is a distinct cuticle and a better developed vascular system in that of the land-plant. Since stomata are present even on the submerged leaves, the only difference is that they remain closed in the water-form. A marked contrast is, however, presented by the leaves of the two forms of *Ranunculus aquatilis* (Fig. 391). Those of the land-form (*L*) have a definite palisade layer, which

occupies the bulk of the mesophyll, and the epidermis is devoid

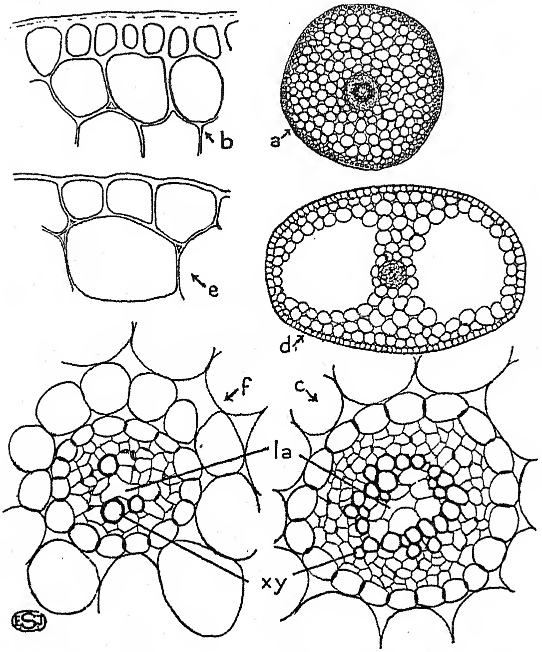

FIG. 390. Transverse sections of the stems of the land- (*a–c*) and water-form (*d–f*) of the Starwort (*Callitriche stagnalis*). *a* and *d*, entire sections; *b* and *e*, epidermis; *c* and *f*, vascular strands. *la.*, lacuna; *Xy.*, xylem-vessels.

of chloroplasts and provided with stomata through which gaseous exchange takes place. In the leaves of the water-form (*W*), on the

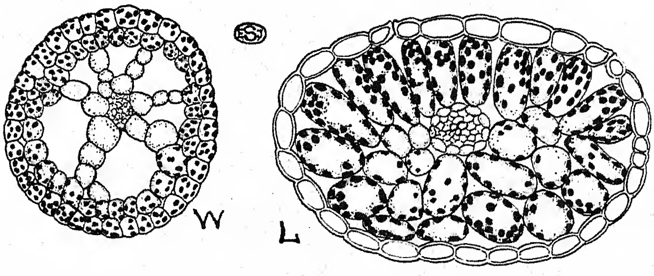

FIG. 391. Transverse sections of the leaves of the land (*L*) and water (*W*) forms of *Ranunculus aquatilis*.

other hand, palisade tissue is absent and there are very conspicuous intercellular spaces. There are no stomata in the epidermis whose

cells contain chloroplasts. Similar differences can be observed between the floating and submerged leaves of this plant, but the anatomical contrast is more striking in the Mare's-tail (*Hippuris*), where the leaves borne above and below water are of the same external form.

A combination of aquatic characteristics with others, usually encountered in the vegetation of dry habitats, is not uncommonly exhibited by plants rooted in boggy ground, but whose shoots are exposed to conditions tending to encourage excessive transpiration. These conditions may in part explain the phenomenon, which is, however, probably an outcome of complex causes. Excellent examples are furnished by the Cotton Grass (*Eriophorum*), the Rush (cf. p. 506), and the Bulrush (*Scirpus*), all typical of such localities. The principal feature reminiscent of aquatics is the vast system of intercellular air-canals which serves to supply the underground organs with oxygen.

A feature of aquatic life is the abundant supply of water and often of mineral salts as well. This enables exceedingly rapid and prolific growth to take place, a fact which is strikingly illustrated by the Canadian Pondweed. This plant (Fig. 404) was introduced into this country in 1847 and spread with such rapidity that at one time it constituted a serious pest by choking up canals and other waterways. In view of this prolific growth vegetative reproduction is generally a marked feature of aquatics. Mere detachment of branches is very common, and such fragmentation is facilitated by the brittle condition engendered by the turgid state of the cells, e.g. *Elodea*, *Ceratophyllum*, both of which only rarely reproduce by seeds.

With the approach of winter many aquatics produce numerous *winter-buds* (Fig. 392), *i.e.* ends of shoots in which the leaves are very closely crowded together and filled with starch (e.g. *Elodea*, Fig. 392, A; *Myriophyllum*, Fig. 392, B); when the parent dies away, these sink to the bottom. In the following spring, with the increase of illumination, the buds sprout and rise to the surface. Such winter-buds resemble the summer-buds (cf. p. 130) of land-plants in having no bud-scales. They are often copiously covered with mucilage formed by secretory hairs.

The buds of *Hydrocharis* and the Water Soldier (*Stratiotes*) are formed at the ends of long more or less horizontal runners, and are produced, not only in the autumn, but also during the summer. Other methods of persistence during the winter are seen in the Duckweed, where entire plants often become full of starch in the autumn and sink to the bottom, and in *Sagittaria*, where small tubers are carried out on branches of the rhizome.

In a mild winter, moreover, many water-plants (Canadian Pond-weed, Duckweed, Water Starwort) persist in an unaltered state.

The bulk of aquatics raise their flowers above the water-level and thus betray their derivation from terrestrial plants. Some are entomophilous (e.g. *Nuphar*). Others are anemophilous (e.g. *Myriophyllum*, Fig. 388; *Potamogeton*, Fig. 291), though occasionally pollinated by insects frequenting the surface of the water (*e.g.* Water-gnats). The peduncles often bend down after flowering is over and carry the developing fruits under water, so that they are well protected (e.g. *Ranunculus aquatilis*).

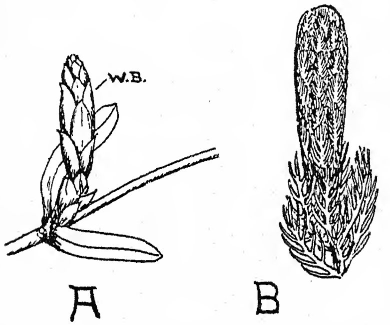

FIG. 392. Winter-buds of A, *Elodea*, and B, *Myriophyllum* (slightly enlarged). *w.b.*, winter-bud.

A few aquatics have become so highly adapted to life in water that even their flowers are submerged. In *Ceratophyllum* these flowers are developed in the axils of the leaves and have a small inconspicuous perianth. They are unisexual with both sexes on the same plant; the male flower has from twelve to sixteen stamens, while the female has a superior ovary with a single ovule. In all such water-pollinated plants the pollen grains are smooth and float readily in the water, currents carrying them to the stigmas; pollination is therefore as uncertain as in anemophilous plants and, in correspondence with this, a considerable amount of pollen is formed. Such water-borne pollen is sometimes highly specialised, that of the Eel-grass (*Zostera*), for example, being tubular, of the same specific gravity as sea-water, and without any cuticularised layer. Many aquatics, which ordinarily raise their flowers above the water, fail to do so if, just before the time of flowering, the water-level rises rapidly; under these circumstances the flower-buds do not open and are cleistogamic (p. 465).

Many of the plants growing by the water-side have fruits which float readily and are not damaged by prolonged submergence. In consequence they become distributed by water-currents.

When vegetation colonises a pond-floor or river-bed, the freedom of water-movement is checked and, as a result, the rate of deposition of water-borne particles is accelerated. These accumulate round the submerged plants with a consequent rise in the level of the bed. The overlying water thus becomes shallower, so that other species can grow and what was once free water

becomes a marsh. The swamp-flora is always encroaching in this manner upon the aquatic vegetation, and in a similar way the reed-swamp, as it becomes more and more dense and the level of the floor rises, is invaded by the marsh-flora. In East Anglia large areas are covered by such dense reed-swamps in which the predominating plants are Grasses and Sedges, *e.g.* Reed (*Phragmites*), Blue Moorgrass (*Molinia*), Reed Canary-grass (*Phalaris arundinacea*), Bog-rush (*Schoenus*), Twig-rush (*Cladium*), etc. A certain amount of peat is formed in such situations, but this contains a large proportion of mineral substance and the soil-water, unlike that of moorlands (cf. p. 536), is often alkaline. This type of community is known as a *fen*. Other characteristic plants are *Lychnis flos-cuculi*, *Valeriana officinalis*, *Ranunculus lingua*, *Thalictrum flavum*, *Ulmaria palustris*, etc.

In this dense fen-community there is a stratification comparable to that in woodlands. Such species as *Valeriana dioica* and *Hydrocotyle vulgaris* form a stratum, equivalent to the ground-flora. In *Ulmaria palustris*, which is a tall-growing species bearing leaves in different strata and therefore subject to decreasing humidity with increase of height above the ground, the lower protected leaves are smooth and green on the under side, whilst the corresponding surface of the exposed upper leaves is of a greyish tinge owing to a thick felt of downy hairs.

Eventually the soil built up by the accumulation of mineral and organic material may become colonised by trees, such as Alder (*Alnus*), Willow, *Rhamnus catharticus*, etc., and a fen-wood or *carr* is produced, which may eventually pass into Oak-wood. We have here again a *succession*, in which one type of plant-community replaces another in a definite sequence, leading to a comparatively stable *climax-community*, the character of which is largely determined by the prevalent climatic conditions.

CHAPTER XLV

VEGETATION OF THE SEASHORE

THE rock-fragments produced by the erosion of the sea coast are distributed through the agency of water and wind. Their capacity for carrying such fragments depends on their velocity. On parts of the coast where wave-action is considerable, reduction in velocity leads to the deposition of the very coarse material as shingle to form shingle-beaches. In quieter waters the finest material is deposited as mud and sand to form salt-marshes, whilst wind-borne sand gives rise above tide-levels to dunes. Exposure to wind is a general feature of coastal situations, shared equally by the beach, sand-dune, and salt-marsh.

Below the level of the lowest tides there is abundant plant-life consisting of large Brown Seaweeds like *Laminaria* and numerous Red Seaweeds; many of the latter grow only in deep water and in their zonation temperature plays an important part. Between tide-levels we often find a rich Seaweed-vegetation, among which Fucaceæ are conspicuous, but there are also a considerable number of Green (*Ulva*, *Cladophora*) and some Red Algæ, the latter usually growing where they are partially shaded. On rocky shores the brown forms show a marked zonation, depending probably on a varying capacity to withstand desiccation.

Pelvetia (Fig. 188) and *Fucus spiralis* occupy the uppermost zone, and many of the plants occur in situations which, except at spring tides, are only reached by spray; the more exposed individuals exhibit a marked dwarfing. Above this spray-belt the cliff-surface constitutes the characteristic home of a number of Lichens and certain Flowering Plants, notably the wild Cabbage (*Brassica oleracea*), *Spergularia rupestris*, *Crithmum maritimum*, and *Inula crithmoides*. Below the level of the spray-belt the intertidal region is occupied in the upper part mainly by *Fucus vesiculosus* (Fig. 186), often accompanied by the related *Ascophyllum*, whilst *Fucus serratus* (Fig. 187) is more abundant in the lower part of this zone. A very typical Seaweed at low-tide level on exposed coasts is another member of Fucaceae, *Himanthalia*, with forked strap-like fertile thalli.

The abundant mucilage of Seaweeds helps to retain moisture and so minimises the effect of alternate submergence and drying up to which all forms living between tide-limits are exposed.

The *Beach* itself, above high-tide level, is not infrequently composed of more or less water-worn fragments or pebbles forming a fringe of shingle to the shore (*e.g.* at Pevensey) or constituting a bar or spit (*e.g.* Chesil Bank, Hurst Castle Bank). Inhospitable as these situations seem, exposed to the full force of the wind, and with a barren soil composed of shingle, sand, and a small amount of drift (*i.e.* plant-remains cast up by the sea or from salt-marshes), yet these habitats are the chief home of many plants that are almost or entirely confined to such localities. Amongst the commonest may be mentioned the Yellow Horned Poppy (*Glaucium luteum*), Wild Beetroot (*Beta maritima*), Sea Campion (*Silene maritima*), Sea Purslane (*Arenaria peploides*), and Crisped Dock (*Rumex crispus* var. *trigranulatus*); more locally *Suæda fruticosa*, Sea-kale (*Crambe*), and the Maritime Pea (*Lathyrus maritimus*) are conspicuous features. Most of these plants have deep roots and fleshy leaves.

The controlling conditions upon the shingle-beach are primarily those of the soil with its extreme mobility,[1] small amount of humus, and lack of capacity for water-retention. The plants inhabiting a pebble-beach are at times partially buried under the shingle carried up during storms, and their presence in such habitats is only possible owing to their capacity for growing through to the new surface. The vegetation appears to depend for its existence largely upon a regular supply of humus to the shingle and, as a consequence, fringing banks which only receive a small amount of drift from the sea are often very bare, whilst those forming a bar or spit exhibit more extensive vegetation, as a result of the more abundant humus derived mainly from the marshes behind.

If we place our hand on a shingle-beach on a sunny day, the surface-pebbles will be found to be quite hot, but if these are scraped away the pebbles below feel cool and are often wet with moisture that is not salt to the taste. Owing to the loose character of the shingle, it is a poor conductor of heat, so that the radiant energy falling on the surface is not appreciably transmitted to lower levels. The hot air between the surface pebbles rises and these convection currents draw in warm moist air, from over the sea or adjacent marshes, which impinging on the cool stones of the interior leads to condensation or so-called *internal dew-formation*. This is an important source of water-supply to the vegetation, especially as it is most plentiful in sunny weather when there is no rain.

[1] Where the shingle is relatively stable, small Lichens of a black or grey colour often cover the surface of the pebbles (cf. p. 341).

The vegetation is mainly perennial and of low, mat-like, growth, only developing tall erect stems, if at all, at the time of flowering. After the seeds are shed the upper parts die away, so that during the stress of winter and the winds of early spring the foliage appears either as a rosette closely pressed against the ground (*e.g.* Horned Poppy), or takes the form of winter-buds situated upon the subterranean portion of the stem (as in *Arenaria peploides*).

The *sand-dune* (Fig. 393–4) has much in common with the shingle-beach, also showing internal dew-formation, but the smaller size of the particles, which include many calcareous shell-fragments, whilst rendering the soil more retentive of water, vastly increases its mobility. This shifting character is indeed a prime factor determining the vegetation.

In any locality where sand-hills abound (*e.g.* Southport, Braunton) it will be noticed that those nearest the sea are small and bear very little vegetation (Fig. 393); as we pass landwards, however, the dunes become larger and merge one into another, whilst the clothing of vegetation becomes more and more complete. The foremost dunes in which the sand is still readily moved by the wind are spoken of as *shifting* or *yellow dunes.* Here, as in the shingle-beach, it is the surface-layers that are transported when the requisite velocity is attained. Nearly all the plants found upon these young dunes are perennial and capable of repeated growth, when buried by the wind-borne sand. Any dead object projecting above the surface will check the speed of the wind and cause some of its burden to be shed. But the pioneer plants as they grow offer an increasing obstacle to the wind and so, increasing deposition, bring about a rise in level.

In the earliest stages the first small heaps of sand usually collect around plants of the Marram-grass (*Psamma arenaria*, Fig. 393), the Sea Couch-grass (*Agropyron junceum*), or, less frequently, the Lyme-grass (*Elymus*); the Marram-grass is much more sensitive to sea-water than the Couch-grass, so that the latter can form dunes lower down the shore. As layer upon layer accumulates, the shoots of the Grasses become successively covered, but no sooner does this take place than further growth from the rhizomes is stimulated and fresh tufts of leaves are formed at the surface (cf. Fig. 395). These not only accelerate deposition, but provide protection against removal.

The same process goes on repeatedly, each fresh layer of sand thus becoming bound to those beneath, so that the enlarging dune is permeated by a skeletal system formed of the branched rhizomes of the Grasses concerned. In this way the whole is knit together and a certain degree of stability is imparted to the extremely mobile

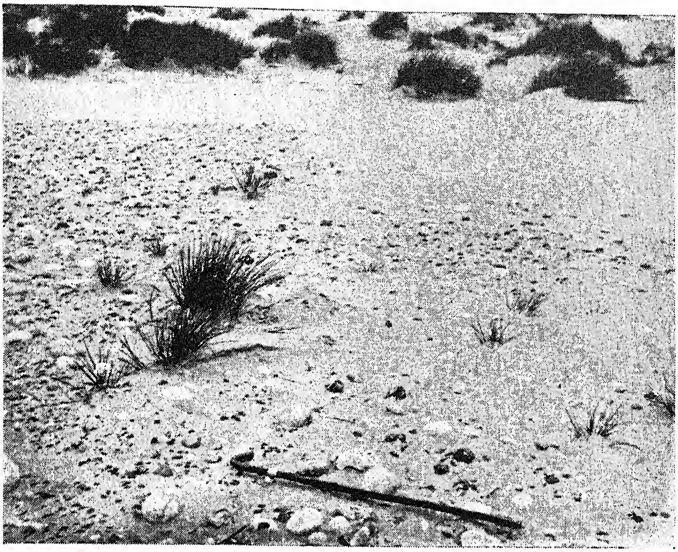

FIG. 393. Young dunes, Blakeney, Norfolk, showing collection of sand behind young plants of the Marram-grass. Older stages are seen in the background. [Photo. E. J. S.]

FIG. 394. "Blow-out" in a dune, Blakeney, Norfolk. The dense covering of Marram-grass is seen in profile, whilst owing to the action of the wind the rhizomes are seen exposed below. [Photo. E. J. S.]

soil-particles. Fresh sand will always tend to collect on the side away from the direction of the prevailing winds, owing to the shelter which the plants and, in later stages, the dunes themselves afford. If strong winds obtain for any length of time in a contrary direction, a considerable quantity of the accumulated sand may be removed and in this way "blow-outs" (*i.e.* excavations in the dune) will be produced, exposing to view the repeatedly branched rhizomes of the Grasses (Fig. 394), the older parts of which are, however, dead.

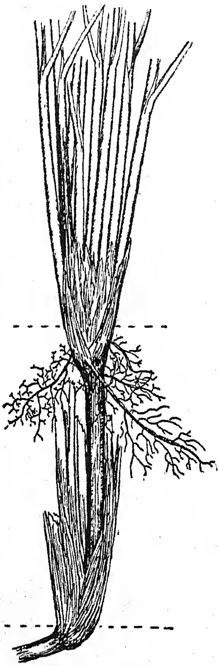

FIG. 395. Portion of a plant of *Psamma* (about one-half natural size), showing leaf-production at successive levels, of dune-surface, these levels being indicated by dotted lines.

Other plants that act as sand-binders are the Sea Holly (*Eryngium*), Sea Convolvulus (*Convolvulus soldanella*), Sand Fescue (*Festuca arenaria*), and Sand Sedge (*Carex arenaria*), the last two, in virtue of the numerous tufts of foliage arising from their horizontal creeping rhizomes, tending to stabilise the surface-layers. The sea-front of the dunes, where there is abundant humus due to drift, is usually inhabited by the Sea Rocket (*Cakile maritima*), Prickly Saltwort (*Salsola kali*), and Orach (*Atriplex* spp.).

On the slightly older and more *fixed dunes*, which are lower than the yellow dunes, numerous shallow-rooted annuals are generally to be found, especially on the lee side. These germinate in the autumn and pass through their life-cycle in the winter and spring, whilst surface-moisture is plentiful, and dry up with the advent of summer. Examples are furnished by species of Mouse-ear Chickweed (*Cerastium tetrandrum* and *C. semidecandrum*), Lamb's Lettuce (*Valerianella*), Whitlow-grass (*Erophila verna*), *Myosotis collina*, *Phleum arenarium* (Fig. 396), etc. Unlike the perennials, these do not exhibit repeated growth, but this is the less essential since the superficial moisture during the few months of their existence tends to "lay" the fine sand at the surface, which latter they themselves protect against the wind. At this phase Mosses, particularly *Tortula ruraliformis*, add to the vegetation carpet.

As the dunes become more stable, other plants, less tolerant of mobile sand, begin to appear upon the lee face, gradually creeping

to the windward side as this becomes sheltered by the dunes in front. Amongst such plants are *Sedum acre*, *Galium verum*, *Senecio jacobæa*, *Erodium neglectum*, *Lotus corniculatus*, *Rosa spinosissima*, *Ononis repens*, and *Taraxacum erythrospermum*. At a relatively advanced stage in dune-fixation numerous Lichens (e.g. *Cladonia* spp., *Peltigera*) appear and their presence gives the sandhills a general grey colour. Hence fixed dunes are sometimes

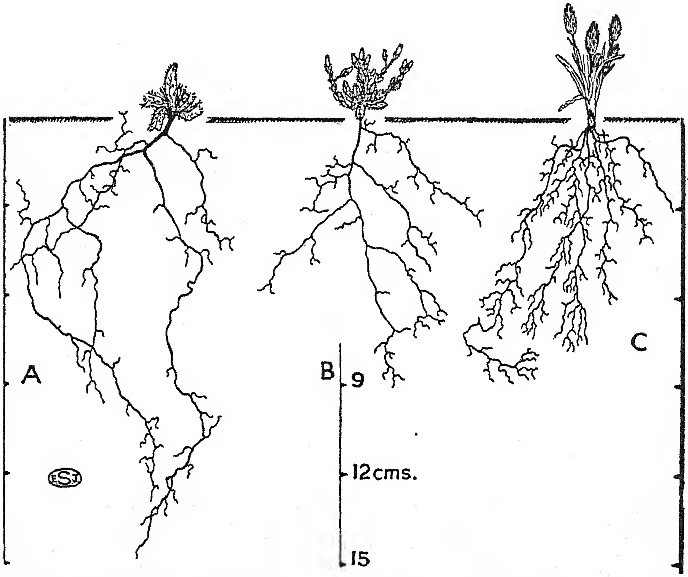

FIG. 396. Root-systems of dune annuals, showing the shallow depth of penetration. A, *Myosotis collina*. B, *Cerastium semidecandrum*. C, *Phleum arenarium*. (After Salisbury.)

spoken of as *grey dunes*, in contrast to the mobile or yellow dunes. Eventually a scrub may form upon the dunes in which the Sea Buckthorn (*Hippophaë rhamnoides*), Elder (*Sambucus*), Bittersweet (*Solanum dulcamara*), Brambles, and occasionally Privet, are conspicuous forms. Between the dune-ridges moisture tends to accumulate, constituting what are termed *dune-slacks*, and here a marshy type of vegetation is established with Creeping Willow (*Salix repens*) as a common species. Here too, as on some of the dune-ridges of intermediate age, characteristic calcicole species are frequent, through the leaching down of carbonates.

The progressive increase in the number of species is rendered possible by the gradual amelioration of the extreme conditions. Not only does the stability increase but, as the plant population

multiplies, organic matter is continually added to the soil, so that its water-retaining capacity is augmented and its fertility improved. Hand in hand with these changes the soil becomes more acid, as the carbonates in the shell-fragments (p. 558) are removed by leaching.

The changes above described constitute a very definite plant-succession. Owing to its mode of formation in successive ridges parallel to the coast, the sand-dune community is peculiar in that the phases of succession in time correspond to their sequence in space, the youngest being nearest the sea, the oldest inland.

The plants inhabiting the dune are practically all xeromorphic with rolled leaves (*e.g.* the Grasses), fleshy leaves (*e.g.* Stone-crop, Sea Convolvulus), very hairy leaves (Sea Buckthorn, Stork's Bill), spines (Sea Holly, Sea Buckthorn), sunken stomata, etc. This xeromorphic habit is due not only to the poor capacity of the soil for water-retention, but also to exposure to winds and the strong heating of the surface-layers of the sand on sunny days. Most of the perennials inhabiting the dune have deep and extensive (cf. p. 496) roots which thus reach the underground moisture, provided by internal dew-formation. The powdery surface forms a mulch (p. 495), diminishing loss by evaporation from the layers below.

The thick cuticle of many of the dune-plants not only prevents excessive transpiration, but also protects them from injury due to impact of sand-grains. The pioneer Grasses are characterised by a specialised leaf-anatomy that enables the transpiring surface to be adjusted to the water-income. An excellent example is afforded by *Psamma*. A section across the rolled-up leaf is more or less circular in outline (Fig. 397, A), and is bounded on the outer (*i.e.* under) surface by an epidermis provided with a thick cuticle (*Cu.*) and devoid of stomata; within are several layers of rounded thick-walled cells (Fig. 397, B, *m.*). The inner (*i.e.* upper) surface has a corrugated appearance, being produced into a number of longitudinal ridges, each of which is traversed by a vascular bundle (*V.b.*). The intervening grooves are flanked by photo-synthetic tissue consisting of more or less rounded cells (*A.t.*). The scattered stomata (*S.*) correspond in position with this tissue and are consequently confined to the furrows, where additional protection is furnished by numerous stiff interlocking hairs (Fig. 397, A).

The epidermal cells at the base of each groove are exceptionally large (*hinge-cells*, Fig. 397, *h.* and *h.c.*) and, being relatively thin-walled, are the first to lose water and shrink when transpiration is excessive. As a result the inner surface of the leaf contracts in width (*i.e.* transversely), so that the flat edges formed by the marginal ridges are brought together, and the leaf as a whole

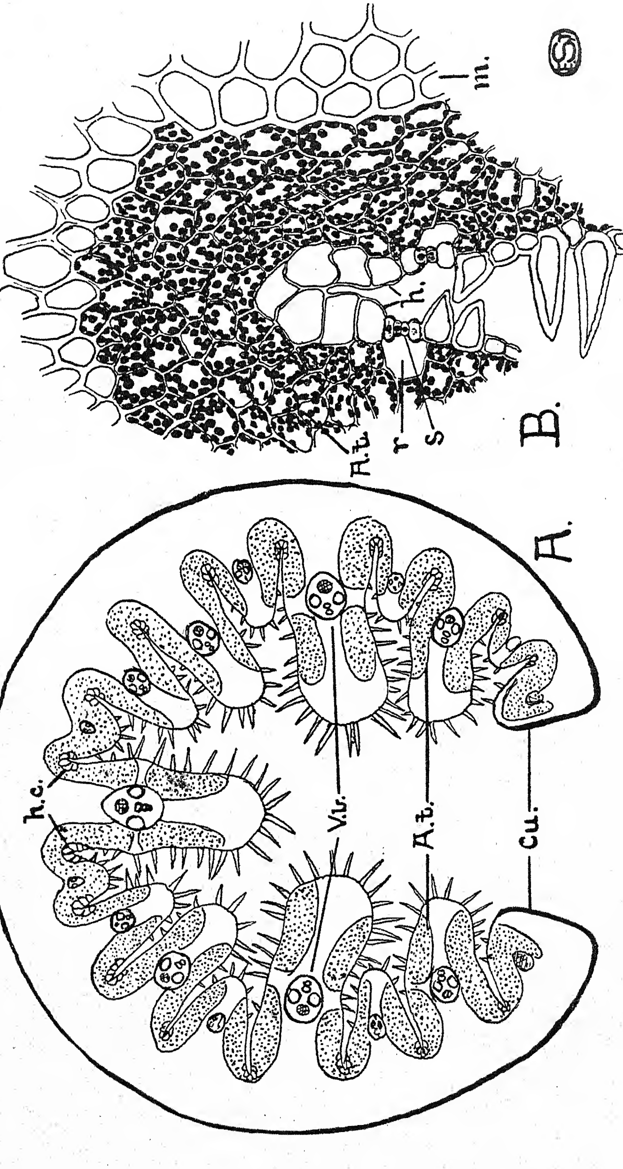

FIG. 397. A, Diagram of transverse section of leaf of Marram-grass (*Psamma arenaria*). B, Small part of one of the grooves, with adjacent tissues, enlarged. *A.t.*, photosynthetic tissue; *Cu.*, cuticle; *h.* and *h.c.*, hinge-cells; *m.*, mechanical tissue; *r.*, respiratory cavity; *S.*, stoma; *V.b.*, vascular bundles.

becomes tubular. When the water-supply is plentiful the reverse action takes place and the blade becomes flattened.

In the more sheltered situations along the shore (*e.g.* bays and estuaries) large tracts of mud, or mud and sand, intersected by water-channels, frequently accumulate. Such areas which are periodically inundated by the tides constitute the habitat known as the *salt-marsh* (Fig. 398), and are frequented by plants very tolerant of saline conditions (*halophytes*). The first obvious colonisers in these situations are usually annual species of Marsh Samphire or Glasswort (*Salicornia*, Fig. 400) which, however, probably always follow small filamentous Green and Blue-green Algæ that have already to some extent bound together the surface-layers. On the south coast, especially that of Hampshire, the mud-flats are colonised by the Eel-grass (*Zostera*) and the Cordgrass (*Spartina Townsendii*), the latter eventually forming a dense community like a maritime Reed-bed.

The colonising Glasswort impedes the incoming tide and so silt is deposited. With the rise in level the vegetation soon becomes less scanty and several additional species appear, such as the Sea Plantain (*Plantago maritima*), Arrow-grass (*Triglochin maritimum*), Sea Aster (*Aster tripolium*), Sea Blite (*Suæda maritima*), and the Sea Manna-grass (*Glyceria maritima*). As further silt collects and the level of the marsh as a whole rises still higher, the number of species and the density of the vegetation increases; in this intermediate condition (Fig. 398) the Sea Pink (*Armeria maritima*), Sand Spurrey (*Spergularia media*), Sea Lavender (*Statice*), and Sea Mugwort (*Artemisia maritima*) are often found in abundance. Sandy salt-marshes are particularly characterised by the Perennial Glasswort (*Salicornia radicans*), *Glaux maritima*, and Sea Heath (*Frankenia lævis*), all found more especially towards the landward edge. The Silver Goosefoot (*Obione portulacoides*) sometimes invades the more sandy types of salt-marsh, first of all colonising the borders of the creeks (or water-channels) and then gradually spreading over the whole, until the former occupants are almost entirely driven out. In the final stage, when the level of the marsh is such that it is not covered even by the highest tides, a *salt-pasture* is formed, characterised, as the salt becomes leached out, by the presence of such Grasses as Bent-grass, Fescue, etc. Much of the flat land reclaimed from the sea occupies the former site of such salt-pastures (Fig. 399) which have been drained and cut off by dykes from the inroads of exceptionally high tides.

In many salt-marshes some of the plants occupy definite zones, corresponding to frequency of tidal inundation, a feature which is

FIG. 398. Intermediate stage in salt-marsh formation, Hunstanton, Norfolk. The most conspicuous plant is *Armeria maritima* (in flower); the remaining vegetation consists of *Salicornia*, *Statice*, *Plantago maritima*, etc. On the horizon is seen a range of low sand-dunes. [Photo. E. J. S.]

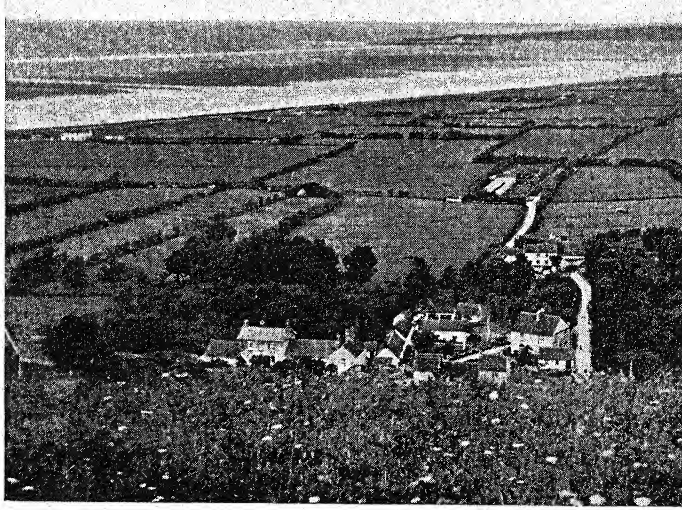

FIG. 399. Reclaimed salt-marshes, Bristol Channel. The flat-lying fields in the middle distance have been reclaimed from the sea. The dark areas in the distance, just beyond the shore-line, are salt-marshes in an early stage of colonisation. [Photo. E. J. S.]

very pronounced where the Sea-rush (*Juncus maritimus*) and *Artemisia maritima* are present. These form fringes at the upper edge of the marsh, the former conspicuous by its height, the latter on account of its white hairy leaves.

Here, again, there is a plant-succession characterised by a small number of highly specialised species giving place to a larger assemblage, as the duration of tidal inundation is diminished.

The soil of a salt-marsh naturally contains a high proportion of chlorides, this being particularly great when evaporation takes place during intertidal periods, and relatively small when the salt becomes washed out by heavy rainfall in the interval between the higher tides. The importance of the latter feature is shown by the very dwarf character of the vegetation of salt-marshes in dry summers. After inundation by the tide the soil is saturated by a solution that has a high osmotic pressure and, as a consequence, the plants of the salt-marsh may readily suffer from physiological drought, *i.e.* a condition in which, though water is present in abundance, it is not readily absorbed by reason of its high content of mineral salts. Actually, owing to an exceptional permeability to chlorides, the osmotic pressure of the cells of the roots of salt-marsh plants tends to vary *pari passu* with that of the soil-solution. Salt-marsh plants are, however, subject to very marked fluctuations of osmotic pressure and are greatly benefited by dilution of the soil-solution by rain-water.

The succulent character of many of the halophytes inhabiting salt-marshes is due to the development of large numbers of water-storing cells (aqueous tissue, cf. p. 510). This is well seen in *Salicornia* (Fig. 400) in which the opposite leaves ensheathe the stem and give the plant a jointed appearance, the flowers being embedded in threes in the tissue of the shoot (cf. Fig. 400). This succulence appears to be related to the presence of salt in the soil, since a considerable number of plants develop a similar fleshy habit when growing in saline situations (*e.g.* Bird's-foot Trefoil, *Plantago coronopus*). The majority of salt-marsh plants are perennials, although *Salicornia herbacea* and *Suæda maritima* are summer annuals.

It has been stated that the salt-marsh soil may be either sandy or muddy in character, with varying proportions of organic silt. This depends on the nature of the tide-borne material to which that brought down by streams into the estuary contributes. When the salt-marsh is muddy, the conditions of aeration for the root-systems may be poor and then the *Salicornias* not infrequently develop aerenchyma (Fig. 401), comparable to that of plants of the fresh-water marsh.

This brief account of plant-communities may be concluded by a consideration of the processes of *colonisation*. Wherever fresh soil is exposed (*e.g.* land-slides, railway embankments, quarries, Fig. 402), it sooner or later becomes covered with vegetation, and in this succession various phases are again recognisable. Very frequently Lichens and Mosses constitute the pioneers, particularly where the subsoil is sand or rock, and play an important part in forming the first humus.

The first Flowering Plants to appear, either simultaneously with

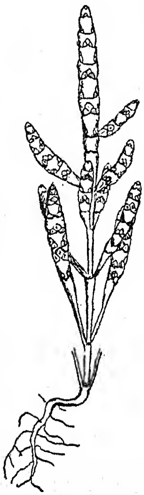

FIG. 400. Small plant of the Glasswort (*Salicornia*, about two-thirds natural size).

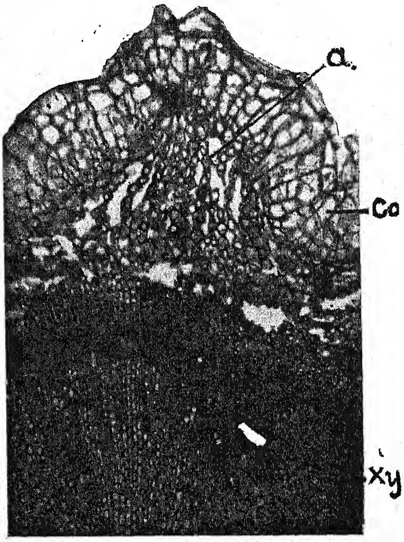

FIG. 401. Photomicrograph of a small portion of the aerenchyma (*a*) of the Marsh Samphire (*Salicornia*). *Co.*, cortex; *Xy.*, xylem. [Photo. E. J. S.]

or subsequent to the pioneers, are usually annuals, which grow in the adjacent districts and possess a good dispersal-mechanism (e.g. *Poa annua*, *Senecio vulgaris*, etc.). The broken surface of arable land (cf. p. 532) may be said never to get beyond this early phase in the succession. In later stages of natural colonisation an increasing number of perennials are found, these gradually ousting the annuals by competition, the order of their appearance often corresponding to the efficiency of their means of dispersal (*e.g.* Grasses, Willow-herbs, numerous Compositæ, Creeping Buttercup, etc.).

In early stages of all successions the vegetation is open, *i.e.* there are considerable areas of bare ground between the plants,

which latter are few as regards the number of species. Subsequently the vegetation becomes denser and denser, and for a time we have a relatively large number of forms battling for supremacy, until eventually the successful ones alone hold the field, these being mainly perennials. If the soil remains undisturbed, shrubs and trees will after some time begin to assert themselves (Fig. 402), and thus we may ultimately get a dense scrub, analogous

FIG. 402. Colonisation of a disused quarry, Yorkshire. In the foreground are Ferns, Furze, Brambles, Wood-sage, etc. The barer parts are only occupied by Mosses and Heather. In the background are bushes of Broom. [Photo. E. J. S.]

to that described on p. 526, or even woodland. A similar succession from an open to a closed community has been noticed above in our description of the succession on sand-dunes and salt-marshes. It will be noted that in general the dominant species increase in size as the succession progresses.

A somewhat analogous series of phases can be observed after the coppicing of a wood (p. 522) or the devastation of a heath by fire. Here two factors come into play, viz. colonisation and sprouting of the underground parts of the woody plants. We may take the reclothing of a burnt *Calluna*-heath as an example. In the first years after a fire a considerable number of species (Rose-bay Willow-herb, Wood-sage, Tormentil, Milkwort, etc.) appear in

large quantity; subsequently as the new shoots sprouting from the shrubby members of the heath-flora (Gorse, Fig. 403, Heather, etc.) assert themselves, these earlier colonisers become more and more crowded out, until finally the original condition is usually re-established.

Each phase of a succession is marked by a definite physiognomy,

FIG. 403. Colonisation of burnt heath, Hindhead, Surrey. The vegetation consists largely of the sprouting stumps of the Dwarf Furze (*Ulex nanus*). [Photo. W. B. Johnson.]

and its members are often characterised by common morphological and anatomical features. Thus, the pioneers on a salt-marsh and arable land are alike annuals, whilst most of the species characteristic of later phases are perennials. The common species in a Callunetum often have small leaves with the stomata confined to grooves, and the plants of a salt-marsh are mostly succulents. Furthermore, we may note that the general trend of succession is to render conditions less specialised, so that the desert-like sand-dune on the one hand, and the water-logged swamp on the other, both come by a sequence of natural changes to approximate to the same type of climax community, namely, woodland.

CHAPTER XLVI

THE GEOGRAPHICAL ELEMENTS OF THE BRITISH FLORA

THE geographical distribution of plants over the surface of the earth is mainly related to differences of climate, the distribution of a species often depending on its tolerance of cold or heat, dryness or moisture, etc. But, apart from such instances in which the range of species is limited by their inability to withstand competition under adverse climatic conditions, certain species, genera, or even families are found to be restricted to particular areas of the earth's surface, though others may also be well suited to their existence. This fact is constantly being illustrated by the successful spread of species after their first introduction into a country. For example, the Canadian Pondweed (*Elodea canadensis*), which was brought to England from America about 1847, now occupies almost every waterway in this country (cf. Fig. 404). A similar phenomenon, on land, is presented by the Prickly Pear (*Opuntia*) in Australia. It may be supposed, in respect to such plants, that the ordinary agencies of dispersal have not sufficed to bring the species to all regions in which it can thrive successfully, though often such extension of range is only possible where human influence has diminished the severity of competition.

The natural barriers to the spread of plants are oceans, mountain ranges, deserts, etc., and it is significant that isolated islands (*e.g.* New Zealand) are peculiarly the home of species, so-called *endemics*, which are found there, and there alone. The capacity of a species to extend its range in new territory depends on an efficient seed-dispersal, the rapidity of its spread by this or by vegetative means, and its vigour in competition with others.

The British Isles afford an outstanding example of the continuous colonisation of an island from the adjacent land masses. They present very varied conditions alike in respect to climate, to geology, and to economic development. In the west the rainfall tends to be high and the climate humid and more equable, whereas in the east the rainfall is low and conditions generally are drier and

more extreme. The south-eastern area is, moreover, a region of dense population and great industrialisation, and has from remote times been most subject to human influence. It is a consequence of

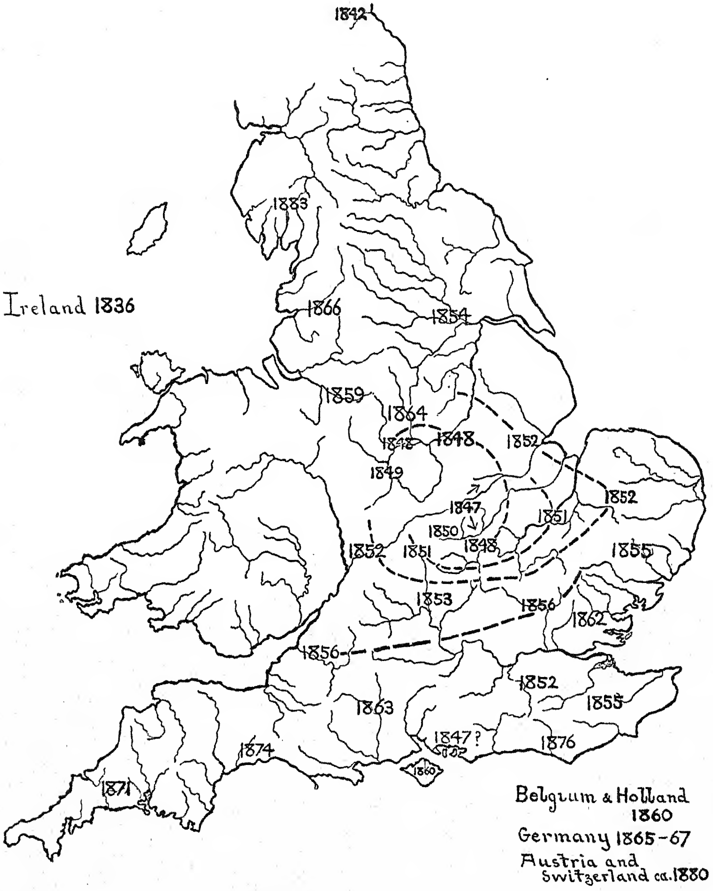

FIG. 404. Map showing the spread of the Canadian Pondweed (*Elodea canadensis*) after its appearance in England in 1847. The broken lines connect identical years.

these facts that, not only does Britain present a wide range of habitat conditions, but there tends to be a segregation into two major environmental regions, the transition zone between which has a general south-west to north-east trend. This is very marked with respect to many southern and continental species (e.g. *Iberis*

amara and *Muscari racemosum*, Fig. 405) which show a northern limit roughly south of a line from the Bristol Channel to the Wash.

The vascular plants of Britain number some 1500 species, of which probably not more than twenty are endemic. Most of the others are also found on the European mainland, though a few are American species (e.g. *Sisyrinchium angustifolium*). Some of the hardier members of our flora probably persisted from preglacial times in unglaciated areas, but the majority are species that re-colonised this country after the retreat of the ice. This process of colonisation has doubtless been a continuous one from post-glacial times to the present day. Evidence furnished by seeds, pollen grains, leaves, etc., preserved in peat, indicates a succession of climatic changes, each of which would have favoured the establishment of species with particular environmental preferences.

In the earliest post-glacial times (the preboreal period) the vegetation would seem to have been tundra-like in character with a preponderance of Dwarf Birch (*Betula nana*), Dwarf Willows (e.g. *Salix herbacea*, *S. reticulata*), *Dryas octopetala*, and other species, such as are common in Arctic regions to-day. The later part of the pre-boreal period was marked by the development of extensive Birch-woods, perhaps of a scrubby character, in which Pines became more and more conspicuous, leading to a Pine-maximum. The boreal period which followed was characterised by climatic conditions typical of continental areas, namely, relatively low humidity and extremes of temperature. During this period *Pinus* diminished in frequency and the Hazel attained a predominant position, although Birch and Pine were probably still common.

In the succeeding phase the climate would appear to have entirely altered; it was markedly oceanic with a relatively high humidity and mild conditions. This Atlantic period witnessed the development of extensive mixed woods of Oak with Birch, Elm, Lime, and Hazel. The high humidity of this epoch favoured increase of the Alder that had now immigrated into Britain, whilst the equable climatic conditions were responsible for woodlands attaining, during this Atlantic period, their altitudinal maximum, marked to-day perhaps by the upper limit of communities of *Calluna* in Britain and of species of *Rhododendron* in the Alps.

A return to more continental conditions characterised the succeeding sub-boreal period, after which an oceanic climate returned in a less marked degree, constituting the sub-Atlantic period, when the Beech and Hornbeam probably first immigrated into Britain.

During the earlier part of post-glacial times nomadic palæolithic man may have occasionally set fire to forests to augment the

pasturage for the grazing animals which he hunted. His rather crude implements were unsuited to the felling of timber, and indeed his activities in this direction would normally involve the cutting of mere firewood of small girth. However, with the advent of neolithic man, who was an agriculturist, permanent destruction of forests began, affecting especially, until the age of metals, the softer timber trees such as Pine and Birch. The felling of *Pinus sylvestris* by neolithic man probably accelerated, if it did not actually cause, the disappearance of natural forests of this species in the greater part of England and Ireland.

The smelting of iron made enormous demands on wood for the manufacture of charcoal, and is known to have been a prime cause of the disafforestation of the Weald of Kent. As an outcome of the extension of agriculture, the growing demand for pasturage to serve the flourishing wool-industry, and the ever-increasing fuel-requirements until the general adoption of coal, the extensive forests of former times are to-day represented by mere remnants. Despite this, however, the high proportion of woodland species in the existing flora of Britain is a witness to the former importance of this type of habitat.

The large areas of grasslands, moorlands, and heaths, which occupy erstwhile forest regions, provide for the species of the former habitats a much more extended area than in primitive times. The increase of habitations and the creation of a network of roads, canals, and railways in more modern times again have furnished open communities of plants by their sides, permitting of colonisation by newly introduced species, many of which maintain but a precarious tenure, whilst others become permanent features of our flora.

The distinction between native and introduced species is rather arbitrary, being a difference of degree rather than of kind. It is, however, of importance to recognise that, whilst many species of our flora flourish in wild habitats enduring the full rigour of competition, others only persist where, as in arable fields, waysides, etc., artificial interference by man restricts biotic factors. Most so-called native species belong to the former category, those known to have been introduced mostly to the latter. But some, recorded as definite immigrants in recent years, such as *Elodea canadensis* and *Impatiens fulva*, can flourish in communities where competition is severe and unrestricted.

We can recognise in our flora various geographical elements, each of which is characterised by certain marked environmental preferences, as shown by the distribution of the constituent species on the European mainland. The presence of these groups are

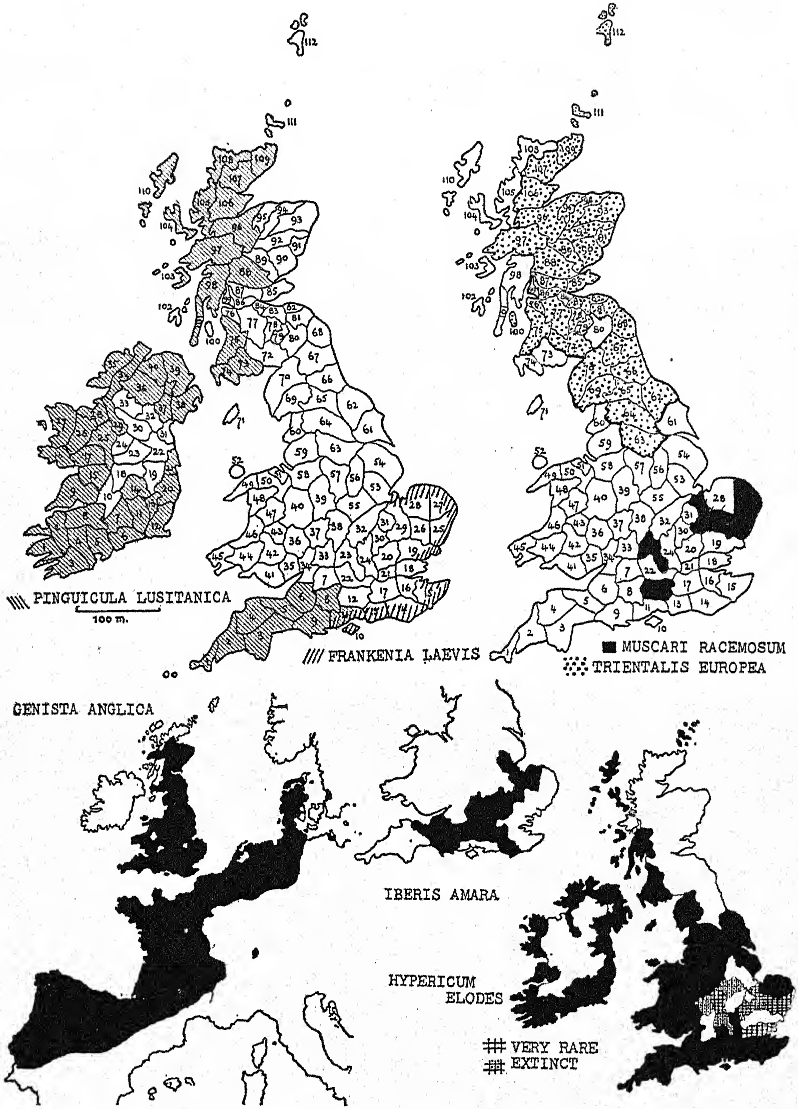

FIG. 405. Maps showing types of distribution in the British Flora. Oceanic types are represented by *Genista anglica*, *Hypericum elodes*, and markedly oceanic types by *Pinguicula lusitanica*. The continental type is represented by *Muscari racemosum*. Southern types are represented by *Iberis amara* and the Mediterranean *Frankenia lævis*, whilst *Trientalis europea* is a northern species. (After Salisbury.)

perhaps reminiscent of the striking climatic vicissitudes of the past, to which reference has already been made. For instance, there are in our flora some 100 species that are normal constituents of Arctic and sub-Arctic vegetation. With the rising tide of temperature after the boreal period, these were left stranded on the summits of our higher mountains, isolated by the sea of lowland warmth. Examples of such Arctic relics, which persist to the present day, are furnished by *Salix herbacea*, *Saxifraga oppositifolia* (Fig. 406), and *Dryas octopetala*. Even more striking perhaps is the small Alpine element, of which *Gentiana verna* and *Cherleria sedoides* furnish examples. This comprises about nine species, which do not occur in northern regions, but are characteristic of the Alps of Southern Europe and which may well have been enabled to cross the intervening plains by the cold of the glacial period. Amongst the more frequent species of the "Northern Element" in Britain may be mentioned the Globe Flower (*Trollius europæus*), the Bird's-eye Primrose (*Primula farinosa*), and *Trientalis europæa* (Fig. 405).

The large oceanic component of our flora is composed of species mainly found in Western Europe and often absent from the drier eastern side of Britain. Their northern limit tends to approximate to a line extending from the north-west to the south-east. Colonisation by and spread of these species was probably favoured during Atlantic times. In this group we can recognise a markedly oceanic element, the species of which are restricted to the Atlantic seaboard of Europe, and especially to that of the Iberian Peninsula. This is sometimes termed the Lusitanian element and in Britain has its chief home in the West of Ireland, the Cornish Peninsula, and Dorset. It includes the Cornish and Dorset Heaths (*Erica vagans* and *E. ciliaris*, Fig. 406), *Pinguicula lusitanica* (Fig. 405), *Scilla verna*, *Ranunculus lenormandi*, etc. A less restricted element, but still definitely oceanic, comprises such species as *Genista anglica* (Fig. 405) and *Erica cinerea*, whilst the Wild Hyacinth, though definitely western, extends as far east as Germany.

The southern component in our flora includes a Mediterranean group, of which *Suæda fruticosa*, *Frankenia lævis* (Fig. 405), and *Statice reticulata* furnish examples. The southern element, in a less restricted sense, comprises plants especially found in southern England, and includes many cornfield weeds, such as *Antirrhinum orontium*, *Anagallis cœrulea*, and *Silene anglica*.

On the sandy heaths of East Anglica the porous soil and the low rainfall, which is often under twenty inches, combine to produce conditions simulating those of Central Europe. The plants of this

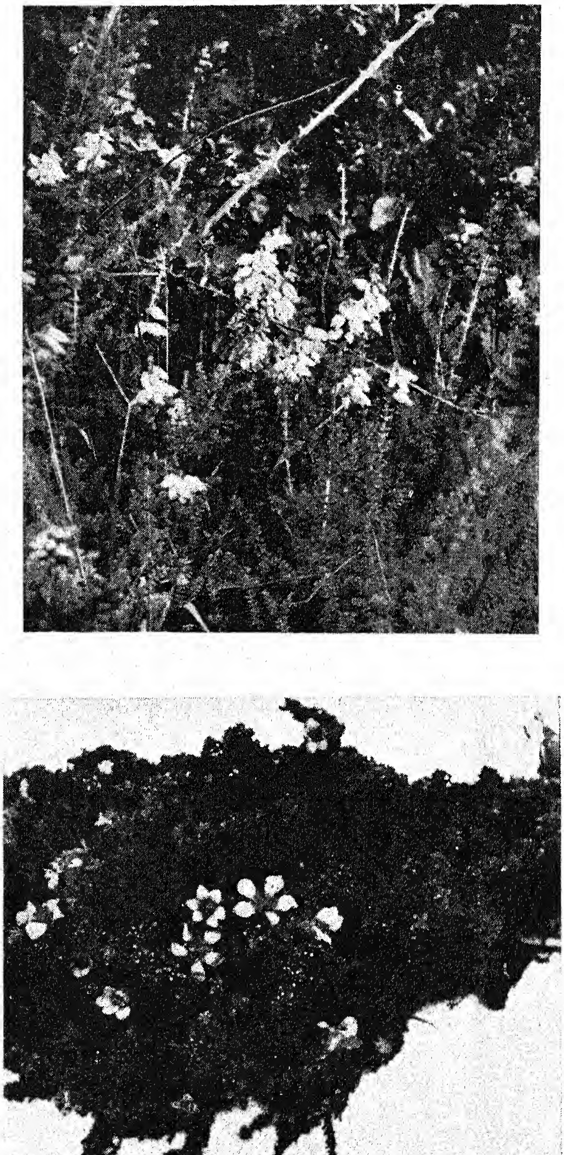

FIG. 406. Above, *Erica ciliaris* (oceanic type); below, *Saxifraga oppositifolia* (Arctic relic).

"continental element" embrace a number of mostly rare species, such as the Grape Hyacinth (*Muscari racemosum*, Fig. 405), *Phleum phleoides*, and *Silene conica*.

A large number of native plants (about half our flora) have a wide distribution on the Continent and, in Britain, mostly exhibit no very marked climatic preferences. The great variety of soils, due in part to a wide geological range, and the absence of a highly differentiated climate, have combined to favour the establishment of species from diverse habitats, and, as we have seen, from a variety of sources. Accretions to our flora continue, but whilst most persist only in semi-artificial habitats, some like the hybrid *Spartina townsendii* or *Mimulus langsdorfii* remain as permanent constituents of natural or semi-natural communities.

The number of species known to have been lost to the British flora is very small, including only a very few marsh-plants, though a large number have disappeared during the past hundred years from some of their former localities. Among such diminishing species plants of wet habitats are the most frequent, a feature associated with a general lowering of the water-table. On the other hand, man's activities, resulting in a marked increase in the area of disturbed soil, has promoted the temporary establishment of many aliens.

The British flora is much less rich in species than that of the European mainland, as is indicated by the fact that in France some 4000 vascular plants are to be found. So too the flora of Ireland contains fewer species than England and Scotland. There are only about 1000 species of vascular plants in Ireland, and amongst the commoner English species which are absent may be cited *Genista anglica* (cf. Fig. 405), the Rest Harrow (*Ononis spinosa*), *Scabiosa columbaria*, and *Avena pratensis*. Others, such as the Rock Rose (*Helianthemum vulgare*), *Geranium pratense*, and *Adoxa moschatellina*, which are widely distributed in England and Scotland, are rare in Ireland. On the other hand, there are about a dozen species found in Ireland that do not occur in Britain; such are the Mediterranean Strawberry Tree (*Arbutus unedo*), *Erica mediterranea*, and *Dabœcia polifolia*, as well as the American *Sisyrinchium* and *Spiranthes gemmipara*. Most of these floristic differences are probably due to greater climatic specialisation and other environmental factors in Ireland, rather than to inadequacy of dispersal.

For further details on HISTORY AND DISTRIBUTION OF THE BRITISH FLORA, see:

CLEMENT REID, *The Origin of the British Flora*, 1899 (191 pp., out of print), which gives a useful summary of the recent geological history of the vascular plants of Britain.

E. J. SALISBURY, *The East Anglian Flora*, Norfolk and Norwich Nat. Soc., 1932 (173 pp.), a study of comparative plant-geography in relation to the whole British flora, including distribution maps of over a hundred species.

E. J. SALISBURY, *The Influence of Man on Vegetation.* Trans. South-Eastern Union Scient. Soc., 1933 (17 pp.).

R. L. PRAEGER, *The Botanist in Ireland*, Hodges, Figgis & Co., Dublin, 1934 (250 pp.), an attractive account of plant-distribution in Ireland, including comital data.

H. C. WATSON, *Topographical Botany*, 2nd edit., London 1883 (612 pp.); together with the two supplements (*Journal of Botany*, 1905 and 1929–30), gives the comital and vice-comital records for England and Scotland.

A. WILSON, *The Altitudinal Range of British Plants.* T. Buncle, Arbroath, 1931 (105 pp.).

The following are standard FLORAS for the diverse classes of British plants:—

(a) *Spermaphyta* and *Pteridophyta*

H. D. HOOKER, *The Students' Flora of the British Isles.* Macmillan & Co., 1930.

C. C. BABINGTON, *Manual of British Botany* (revised by A. J. Wilmott), 1922.

G. C. DRUCE, *Hayward's Botanists' Pocket Book.* Bell & Sons, 19th edit., 1930 (useful in the field).

W. H. FITCH and W. G. SMITH, *Illustrations of the British Flora.* L. Reeve, 1924.

R. W. BUTCHER and F. E. STRUDWICK, *Further Illustrations of British Plants.* L. Reeve, 1930.

For CULTIVATED PLANTS, see:

W. J. BEAN, *Trees and Shrubs hardy in the British Isles.* Murray, 3 vols., 1925–1936.

J. W. C. KIRK, *A British Garden Flora*, Arnold, 1927 (584 pp.), which provides a key for the identification of the genera of cultivated plants.

For the identification of ALIEN SPECIES occurring in Britain, the *Illustrated Flora of the Northern States and Canada*, by BRITTON and BROWN (Scribner, New York, 3 vols., 2nd edit., 1913), will be found most helpful for American species. Of the standard European Floras, the most generally useful is perhaps COSTE'S illustrated *Flore de France* (3 vols., Paris, 1906, reissue with supplement, 1938), which, covering as it does the whole of France and its borders, as well as Corsica, and illustrating upwards of 4000 species, will serve to identify most species of European origin likely to be found in Britain, and contains most species likely to be found when travelling in Western Europe. Visitors to Switzerland should consult the well-illustrated work, *Das Pflanzenleben der Alpen*, by K. SCHROETER (2nd edit., 1288 pp.), and *Die Vegetation der Schweiz*, by H. BROCKMANN-JEROSCH (1929, 499 pp.).

(b) *Bryophyta*

H. N. DIXON and H. G. JAMESON, *The Student's Handbook of British Mosses*. 2nd edit., V. V. Sumfield, Eastbourne, 1904.

J. B. DUNCAN, *A Census Catalogue of British Mosses*, 2nd edit., Berwick, 1926 (66 pp.), which gives comital and vice-comital distribution.

W. R. SHERRIN, *An Illustrated Handbook of the British Sphagna*. Taylor & Francis (74 pp.).

S. M. MACVICAR and H. G. JAMESON, *The Student's Handbook of British Hepatics*. 2nd edit., V. V. Sumfield, Eastbourne, 1926 (figures of all species).

W. INGRAM, *A Census Catalogue of British Hepatics*. Darwen, 2nd edit., 1913 (35 pp.), which gives distribution data.

(c) *Algæ*

G. S. WEST and F. E. FRITSCH, *A Treatise on the British Freshwater Algæ*, Cambridge Univ. Press, 1927, a useful general account and suitable for the identification of genera. For the identification of species, see A. Pascher, *Die Süsswasserflora Deutschlands, Oesterreichs und der Schweiz*, in several vols., Jena, 1914 and onwards.

W. WEST and G. S. WEST, *British Desmidiaceæ*, Ray Society, 1904–1923, 5 vols. (vol. 5 edited by N. Carter), which gives figures of all species.

G. M. SMITH, *Freshwater Algæ of the United States*, McGraw Hill Book Co., 1933, also useful for the identification of genera.

W. H. HARVEY, *Phycologia Britanica*. London, 1846–51 (Coloured plates of most British Seaweeds).

L. NEWTON, *A Handbook of British Seaweeds*. Brit. Mus. Publ., 1931 (illustrated).

W. R. TAYLOR, *Marine Algæ of the North-eastern Coast of North America*. Univ. of Michigan Press, 1937 (illustrations of many Seaweeds).

J. GROVES and G. R. BULLOCK-WEBSTER, *British Charophyta*. 2 vols., Ray Society, 1917 and 1924 (Figures of all species).

(d) *Fungi*

J. RAMSBOTTOM, *A Handbook of the Larger British Fungi*. Brit. Mus. Publ., 1923 (illustrated).

CARLETON REA, *British Basidiomycetæ*. Cambridge Univ. Press, 1922 (799 pp.).

W. B. GROVE, *British Stem and Leaf-Fungi* (*Cœlomycetes*). Cambridge Univ. Press, 1933 (488 pp.).

W. B. GROVE, *The British Rust Fungi*, 1913 (412 pp.).

A. and G. LISTER, *A Monograph of the Mycetozoa*. Brit. Mus. Publ., 3rd edit., 1925 (296 pp., illustrations of all the species).

A. LORRAINE SMITH, *Handbook of British Lichens*. Brit. Mus. Publ., 1921 (158 pp.).

CHAPTER XLVII

HEREDITY AND EVOLUTION

IT will be a matter of common knowledge that the offspring of either plants or animals resemble their parents very closely.[1] This fact, though so obvious, really involves the fundamental principle of *inheritance.* Thus, if we sow the seeds obtained from a self-pollinated flower of the Foxglove, the numerous resulting seedlings obviously inherit the same general characters. Closer observation, however, shows that there are many minute points of difference which may in the main be related to the fact that the conditions in the seed-bed are not uniform (cf. also Fig. 407). The features presented by any particular individual may, as a matter of fact, be regarded as the outcome or resultant of two sets of factors, being either inherited or due to the effect of environment, that is all the external influences—physical, chemical, and biological—to which the organism is subjected. In plants, and still more in animals, the conditions of the environment are not constant throughout the life of the individual, but in general it is those experienced in the early stages of development which are most potent in moulding the organism.

Individual variations, though probably in the main correlated with differences in the environment, may well also result from changes in the internal conditions which are more difficult to analyse. Such variations may be of two kinds. They are *qualitative* or *substantive*, when, for instance, they concern the shape or size of the entire plant (Fig. 407) or of any of its parts, the degree of hairiness, the type of colouration (Fig. 408), etc. On the other hand, they are *quantitative* or *meristic*, when they involve differences in the number of constituent parts, such as perianth-segments, leaflets in a compound leaf, etc.

It is easiest to study variation if some character is selected which is capable of exact measurement, as, for instance, the length of the leaf in the Privet, the length of the Runner Bean seed, or the number

[1] The reader should consult C. Darwin, *The Origin of Species*. J. Murray, London, 1901 (703 pp.).

of ray-florets in the Daisy. Taking the first of these as an example, it will be found that if, say, a thousand leaves are measured, the difference between the length of the shortest and the longest is quite considerable, and that the majority of the leaves are of an average size. If all the thousand leaves be classified according to their lengths into separate groups, differing by increments of one millimetre, and the number of leaves in each group counted, those containing the smallest number will be found to be situated at the two extremes. Between these points the number of leaves of each particular length will

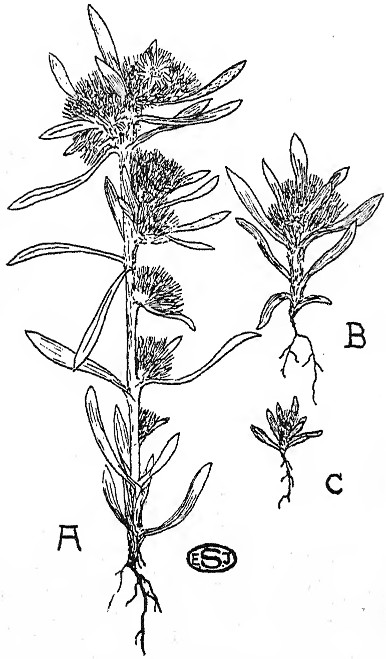

FIG. 407. Three individuals of equal age of the Marsh Cudweed (*Gnaphalium uliginosum*) from the same locality, showing individual variation. All three are in fruit. (Natural size.)

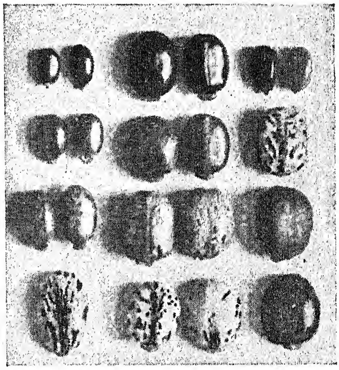

FIG. 408. Seeds of different varieties of Castor Oil (*Ricinus*), to illustrate variation within a species. [Photo. E. J. S.]

be found to increase with considerable regularity, as the size of its individuals approaches that exhibited by the majority. This most frequent size is termed the *mode*, and often corresponds very closely to the arithmetical mean of all the measurements.

By plotting a curve, in which the ordinates represent the number of individuals in each group, and the abscissæ the respective lengths, the variation can be graphically represented (Fig. 409). The larger the number of individuals taken into account, the smoother the outline of and the more symmetrical the curve. Such *variation curves* are most commonly symmetrical (Fig. 409, left), but they

may be one-sided or asymmetrical (Fig. 409, right), as in meristic variation of the corolla-segments of many flowers, where there are often relatively few examples with *less* than the normal number of parts.[1]

The symmetrical curve of variation (normal variation curve) agrees very closely with that representing variation depending on pure chance, a feature which in itself suggests that the manifold differences in the conditions of the environment are involved. The classical example of such chance variation is afforded by the repeated tossing up of two coins, the combination of one head and one tail being most frequent (forming about 50 per cent.), whilst the combinations two heads or two tails occur with about equal infrequency. A more illustrative curve of chance variation would be obtained if ten coins were tossed simultaneously for a sufficiently large number of times.

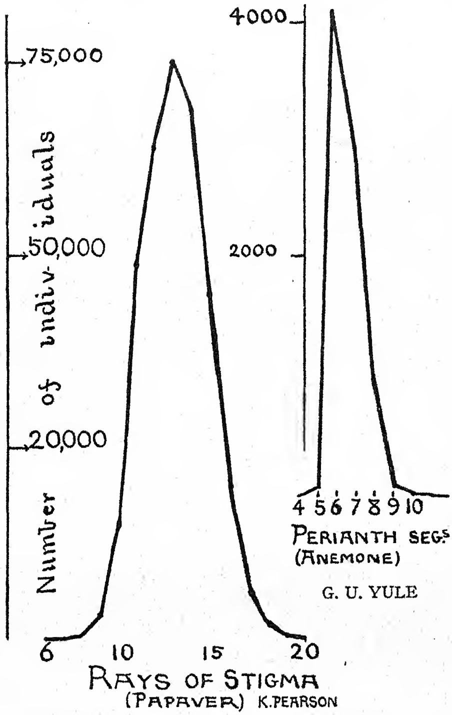

FIG. 409. Variation curves, symmetrical on the left and asymmetrical on the right.

In meristic variation the difference between the extremes is much greater when the mode corresponds to a large number than when it coincides with a small one. Thus, if variation due to fission of parts (say of the corolla of a flower) be equal in two species, the one having a mode of five (*i.e.* usually five petals) and the other having a mode of ten (*i.e.* usually ten petals), there would be just double the chances of fission occurring in the latter as in the former. The extreme condition (*i.e.* 10 and 20 petals) would be attained where all the petals underwent

[1] See G. U. Yule, *An Introduction to the Theory of Statistics*, Griffin & Co., 11th edit. 1937 (570 pp.); R. H. Fisher, *Statistical Methods for Research-workers*, Oliver & Boyd, 1936 (339 pp.).

fission. That is, the range would be greater in the one than in the other, although the actual frequency of fission of the individual segments was the same in the two species. Hence a comparison of variation, where the modes are dissimilar, can only be made by taking such dissimilarity into consideration, a comparison of the curves alone being misleading. The position of the mode can often be to some extent changed by modifying the environmental conditions, although the range of variation remains practically unaltered.

It appears that individual variations are not inherited, and that in a *pure line* of descent the average of the race is maintained.[1] This has been established by sowing seeds from a single individual of pure descent which has been self-fertilised, the seed produced by the resulting plants (likewise self-fertilised) being sown in separate groups, and the same procedure followed for several successive generations. It was thus found that the average size of individuals derived from small parents is practically identical with that of individuals grown from large parents; also that heavy seeds do not beget heavier-seeded offspring than those derived from light seeds. The following data, which serve to illustrate this point, are taken from Johansen's experiments with Beans which were self-pollinated:

Weight of seeds of parents.	Average weight of seeds of offspring.
350–400 mg.	572 mg.
450–500 ,,	535 ,,
500–550 ,,	570 ,,
550–600 ,,	565 ,,
600–650 ,,	566 ,,
650–700 ,,	555 ,,

When dealing with a population consisting of members possessing varied hereditary constitution (*i.e.* not a pure line), a pure strain can often be obtained by selecting individuals which show a particular desired character and breeding from these, with due precautions against cross-pollination. In this way it might, for example, be possible by repeated *artificial selection* amongst the progeny of self-fertilisation to obtain pure lines, exhibiting a given character, *e.g.* a tall or dwarf habit. Under natural conditions the environment may often effect a similar elimination (so-called *natural selection*). The possession of a particular character is sometimes decisive in determining which plant shall survive in the face

[1] By a pure line is understood a pure bred strain produced by self-fertilisation from a single individual. A *clone* is a population produced by vegetative propagation (division) from a single individual.

of competition and adverse habitat conditions. Even in a pure strain, some selective action might lead to the elimination of all but the heaviest, shortest, etc., individuals in each successive generation. This was the essence of Darwin's theory of the origin of new species.

The majority of plants produce such an abundance of either spores or seeds that, even with the most efficient dispersal, it would usually be impossible for more than a fraction of the offspring to become established. Many a common plant would, indeed, if the means of dispersal were adequate, and all the progeny of successive generations survived, rapidly cover a large surface of the globe. That this does not happen is due to that ceaseless competition of living organisms with one another which is known as the *struggle for existence*. A Mullein plant, for example, may produce as many as 700,000 seeds. The resulting seedlings are not of equal vigour, and those first to succumb in the struggle for existence are obviously the weakest. The latter, applying the term in its widest sense, owe their lack of vigour partly to inherited characteristics and partly to adverse environmental conditions. Just as a human being with a "weak constitution" may have inherited his defect or owe it to the surroundings in which he grows up.

Unlike most animals, plants cannot choose their place of habitation. The seeds or spores are carried passively to a variety of situations, and their chances of developing into mature plants depend upon their power of accommodating themselves to the environment in which they may be placed. But many plants exhibit this power of *adaptation* to a very marked degree, as is well illustrated by those aquatics which can grow either totally submerged or on exposed mud (cf. p. 551), by the sun- and shade-forms of woodland plants (p. 521), and by the alpine forms of lowland plants (p. 528, Fig. 370).

It has long been a matter of dispute as to whether or no the changes, impressed upon an organism by the environment, bring about any corresponding internal modification by means of which the new characters can be transmitted to the offspring. So far attempts to demonstrate satisfactorily the inheritance of such *acquired characters* in plants have proved a failure. It is indeed difficult to conceive of means by which characters, acquired by the plant in the course of its lifetime, could affect and modify the hereditary mechanism which must obviously be contained within the fusing gametes. On the other hand, the marked adaptations of plants in the wild state to their normal environment, features often retained when the organism is transferred to another habitat, naturally suggest the possibility of the unstable acquired characters

becoming ultimately stabilised. This view has led to the conception of the origin of new species, etc., through cumulative selection and hereditary transmission of favourable variations (or mutations, cf. below), tending towards more complete harmony between the plant and its environment. Another point, upon which there is

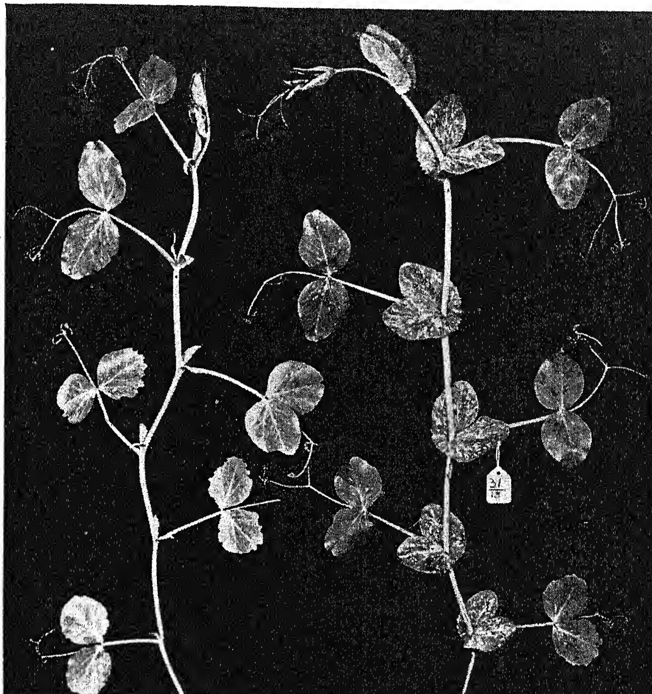

FIG. 410. A new form or mutant which arose from a pure strain of Duke of Albany Pea and which differs in the narrow lanceolate stipules. The type on the right, the mutant on the left. [By permission of the late Prof. Bateson, F.R.S., and Miss Pellew.]

much difference of opinion, is the actual influence of the environment in moulding the structure of a plant. Whilst some consider that adaptation to the environment is due to selection, others believe in a direct response to changed surroundings.

Seeing that the individual variations above considered are all encompassed within the apparently fixed range of the species (cf. p. 583), they could scarcely seem to have led to the evolution of new forms. But in carefully selected and self-fertilised cultures of the higher plants, and even in pure cultures of lower organisms,

it has been found that slight or pronounced departures from the mode occasionally arise which breed true to their new characters from the very outset, *i.e.* these are hereditarily transmitted. Such *mutations*, which are sometimes far more pronounced than the individual variations, and consequently obvious even to superficial examination (Fig. 410), may well be one mode of origin of new species. The causes of mutation are unknown, but it is tempting to assume that the external environment is the stimulus that brings about the internal change. If this could be experimentally proved, many of the divergent views at present held could be harmonised. One form of external stimulus, namely, X-rays, has actually been shown to increase markedly the frequency of mutation.

A familiar instance of a mutation is afforded by the Irish Yew (*Taxus baccata* var. *fastigiata*), which differs from the Common Yew, from whence it arose, in its darker foliage and cypress-like habit. Detailed studies of mutations were first made by De Vries on a species of Evening Primrose (*Œnothera lamarckiana*), which occurred as an escape in a field near Amsterdam, where it was found producing a considerable number of new forms, which subsequently bred true. For instance, one form was distinguished by the possession of broad leaves, another by red-veined leaves, others by dwarf- or giant-habit, and so on, as the following epitome of some of De Vries' cultures shows.

MUTATION IN *ŒNOTHERA LAMARCKIANA*

(The horizontal lines show successive generations, invariably obtained only by sowing seeds of the ordinary form.)

	Giant Form.	White-leaved. Form.	Oblong-leaved Form.	Red-veined Form.	Normal Form.	Dwarf Form.	Broad-leaved Form.
I	—	—	—	—	9	—	—
II	—	—	—	—	15,000	5	5
III	—	—	—	1	10,000	3	3
IV	1	15	176	8	14,000	60	73
V	—	25	135	20	8,000	49	142
VI	—	11	29	3	1,800	9	5
VII	—	—	9	—	3,000	11	—

Since it has been suggested that De Vries' mutants sprang from an originally hybrid stock (cf. below), it may be mentioned that other instances of mutation have since been described in which the pure-bred character of the original strain appears to be beyond question. Moreover, mutations do not occur only in plants raised from seed, where two gametes have been involved. The propagation of *vegetative mutations*, or *sports*, which first appear only on a few branches of the plant, has given rise to the

cut-leaved varieties of Alder, Beech (Fig. 411), etc., the leaves of which are normally undivided.

Another mode of origin of new forms is due to the recombination of characters which takes place when two different races, varieties, or species are employed as the respective parents. In such instances the fertilised eggs are, of course, produced by the participation of both parents, one furnishing the female and the

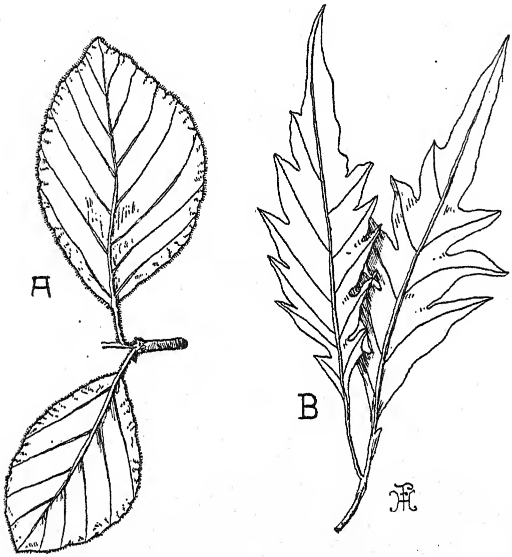

FIG. 411. Twigs of A, ordinary Beech, and B, cut-leaved Beech, illustrating a vegetative mutation.

other the male sexual cell. Such "crossing" is often a failure, no seed being set, but when successful the next generation is an admixture of the characters of the two parents, some features belonging to the one and some to the other.[1]

In respect to any single contrasting feature (*e.g.* height, hairiness, etc.), however, the character of one or other parent frequently altogether predominates (*i.e.* the offspring all show the one feature), although sometimes the *hybrid* is in respect of a given character intermediate between the two (cf. p. 594). Since the characteristics

[1] Important reference-books dealing with hybrids are: W. Bateson, *Mendel's Principles of Heredity*, Cambridge Univ. Press, 1913 (413 pp.); M. B. Crane and W. J. C. Lawrence, *The Genetics of Garden Plants*, Macmillan & Co., 1934 (236 pp.); R. C. Punnett, *Mendelism*, Macmillan & Co., 6th edit., 1922 (219 pp.).

of both parents must have been inherited, those of the one must, in the former instance, be supposed to remain *latent*. Indeed, if such hybrid plants are self-fertilised, the latent character reappears in a certain proportion of the individuals arising from the resulting seeds, a fact which proves that it must have been present, although not outwardly manifest.

A quantitative study of the phenomena of *hybridisation* was first published by Mendel, an Austrian monk, who considered the behaviour of single pairs of characters only. In one of his earliest experiments he crossed tall and dwarf Peas, the whole of the resulting offspring (first generation) being tall. The seeds produced from these, by self-fertilisation, afforded two classes of individuals, three-quarters being tall and one-quarter dwarf. But of these tall Peas of the second generation (if again self-fertilised) only one-third bred true, the remainder behaving just like the original hybrids of the first generation, and giving rise to talls and dwarfs in the proportion of three to one. The dwarfs invariably bred true. In the second generation of such a cross, then, as regards any one particular pair of characters, half the offspring are pure (one quarter resembling one parent, another quarter the other parent), whilst the other half are impure and bear the characters of both. Representing the tall Pea by T and the dwarf Pea by d, these results can be graphically expressed as follows:

First generation: 100% Td (all tall).
Second generation: 25% TT: 25% dd: 50% Td (one tall: one dwarf: two hybrids).

A considerable number of other pairs of characters have been studied in the same way, with identical results, though there are a number of exceptions, some of which are at present inexplicable.

The latent character is usually spoken of as the *recessive* and the other as the *dominant*. In the experiment with tall and dwarf Peas above described, where the difference is one of size, there is reason to believe that the dwarf habit is due rather to the absence of a character causing tallness than to the presence of a special character for dwarfness. And it may well be that in all instances the recessive character is caused by the absence of something which determines the dominant feature (*e.g.* a glabrous form of a particular plant may be due to the absence of a character for hairiness, etc.). Pairs of characters, which thus combine in the first hybrid generation and segregate in the subsequent generations, are termed *allelomorphs*. The following are further examples, the dominant character in each being that first named:

Yellow and green, round and wrinkled seeds in Peas.
Prickly and smooth fruits (Thornapple, Field Buttercup).
Susceptibility and resistance to Rust in Wheat.
Starchy and sugary endosperm in Maize.
Hard (glutinous) and soft (starchy) endosperm in Wheat.

A feature which may be of great significance is that almost all the mutants so far studied behave as recessives to the parent stocks from which they sprang. It may be added that recent research has shown that many apparently simple characters can be analysed into a number of subordinate ones, which, however, are very commonly inherited together.

The most important principle, demonstrated by the experiments of Mendel and subsequent workers in this field, is that the characters introduced by either parent do not become inextricably intermingled in the hybrid offspring, but become separated out again in the gametes; that is to say, each of the latter bears only one allelomorph. It is only on this basis that the reappearance of a latent character in the second generation can be explained. There is reason to believe that in hybrids, during the formation of each tetrad of spores, and in conjunction with the reduction division (p. 314), the determinants of the characters become separated, so that each spore, and consequently each of the gametes, to which it ultimately gives rise, bears one only of each pair of determinants. In the reduction division, therefore, the allelomorphs will become separated so that pure recessives and pure dominants can be bred.

It has been repeatedly noted that the fusion of the nuclei of the gametes appears to be the most important step in *sexual reproduction*. This is supported by the fact that, in all the higher plants, the male cell consists of little else than the nucleus (cf. pp. 422, 469), and that, in hybrid-experiments, it is immaterial whether the one or the other parent is employed as the male.[1] The nucleus has also been seen to play a very important part in the activity of the cell, and, when dividing, to pass through a very complex series of changes. Moreover, the number of chromosomes is usually constant among all the individuals of a species. The division-stages have as their outcome an equal distribution of the chromatic material, which indeed is the only part of the nucleus that remains recognisable throughout all the phases of division (p. 55). The chromatin is thus well suited to be a carrier of the hereditary qualities of the organism. It should, however, be emphasised

[1] Some forms of *Œnothera* and *Epilobium* appear to constitute an exception to this generalisation.

that the chromatin can only exist in a cytoplasmic environment and that inheritance through the cytoplasm, as distinct from the nucleus, has also been established.

It is helpful at this point to consider in greater detail the nuclear changes involved in the reduction division.[1] These differ in several important respects from those observed in the ordinary vegetative divisions (cf. p 55 *et seq.*). In the early prophase of the first division (Fig. 412, A) the nucleus contains a number of long, thin, granular threads which represent the chromosomes. These become associated lengthwise in pairs (B), such pairing being accompanied by a shortening of the threads (C). Later, in each of the paired threads a longitudinal split appears, dividing each chromosome into two *chromatids*, so that each group now consists of four threads. At the time of pairing of the chromosomes, they often, in fixed material, appear aggregated towards one side of the nucleus; this appearance, referred to as *synezesis*,[2] is possibly an artifact.

As soon as the splits between the chromatids appear, the original paired threads (chromosomes) seem to lose their attraction for one another and separate, but not completely, for they are held together at one or more points, termed *chiasmata* (Fig. 412, D). Parts of the paired chromosomes, where there are no chiasmata, seem to repel each other strongly; thus, a chromosome pair with a median chiasma will have the form of an X (cf. Fig. 412, E), of which each limb is, of course, double, whilst where more than one chiasma occurs, the chromosome pairs may present the appearance of a string of lozenge-shaped meshes. The paired chromosomes shorten and thicken (*diakinesis* stage, Fig. 412, E), and these changes accompany the disappearance of the nucleolus or nucleoli. The spindle is constituted, and the paired chromosomes take up their positions at the equator (F). The pairs then separate, one chromosome of each pair passing to either pole (G); as this takes place the paired chromatids seem to repel each other strongly (H).

After a short, or even incomplete, resting period a second division occurs which closely resembles a normal mitosis (Fig. 412, I, J). It will be realised, however, that the half-chromosomes, which travel to the poles in this second division, are actually the chromatids formed by the split which appeared early in the preceding prophase. The two nuclear divisions just described constitute *meiosis* or reduction division, so called because the chromosome number (diploid) characteristic of the vegetative cells is halved. It is important to grasp that it is only the first of these two divisions

[1] See the works cited on p. 54.

[2] Often erroneously referred to as *synapsis*, a term originally applied to chromosome-pairing.

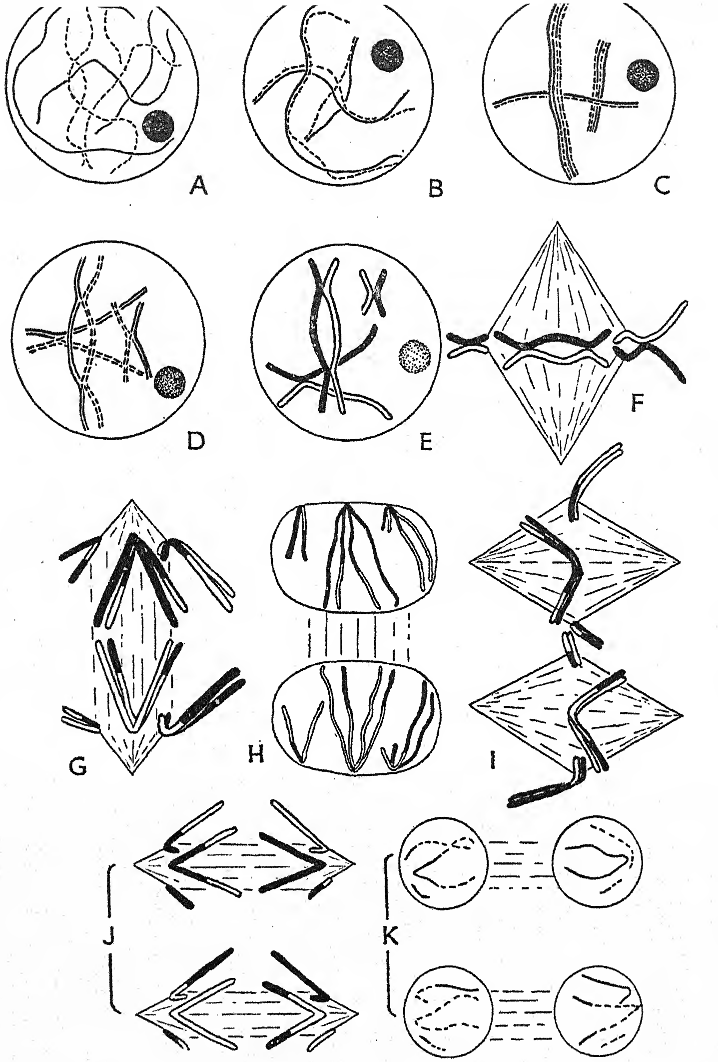

FIG. 412. Diagrams to illustrate behaviour of a nucleus, containing three pairs of chromosomes, at meiosis. One member of each chromosome pair is shown either as a continuous line, or black, the other as a broken line or white.

A, Early prophase of first division, with the chromosomes as six long thin threads. B, Pairing between the chromosomes is beginning. C, Pairing complete, the threads are shorter and thicker. In two of the pairs each chromosome has divided longitudinally into two chromatids. D, The paired chromosomes have separated except at certain points—the chiasmata. E, Diakinesis: the paired chromosomes have shortened and thickened and the separate chromatids are obscured. Nucleolus and nuclear membrane are about to disappear. F, Metaphase, with chromatids still obscured. G, Anaphase showing whole chromosomes in which the chromatids are now obvious passing to the poles; crossing over is supposed to have occurred (cf. p. 595). H, Telophase, with sister chromatids widely separated. I,

which differs materially from an ordinary vegetative division. In all plants, except the Thallophyta (cf. p. 314), meiosis is associated with tetrad-formation in the spore mother-cells. There is good reason for believing that the pairs of chromosomes associated in the prophase of the first division are made up of the corresponding parts of the paternal and maternal nuclei, so that the material brought together in fertilisation is normally re-distributed in reduction. The importance of meiosis is also emphasised by its occurrence in animals, although here it usually takes place during the formation of the sexual cells.

Many inherited characters have been experimentally shown to be associated with definite chromosomes, and in some instances even with particular regions of a chromosome. For this reason particulate representation of the determinants of characters in the chromosomes has been hypothecated and these are referred to as *genes*. It cannot however be too strongly emphasised that the hereditary potentialities influence one another and that the manifested characters are the outcome of the whole gene complex as affected by both the external and internal environments. A gene that brings about certain morphological or physiological manifestations in one gene complex and external conditions may bring about very different effects in others.

In an allelomorphic pair one character (e.g. *the dominant*) is assumed to be present in one chromosome of the pair and the recessive in the other. If the dominant and recessive characters of an allelomorphic pair are represented by A and a respectively, then the fertilised eggs produced by crossing will all have the constitution Aa, and the resulting plants will all show the dominant character only; such individuals are spoken of as *heterozygotes*.

During self-fertilisation, and assuming the gametes to meet according to the laws of chance, there are four possible combinations: viz. (1) a male gamete bearing A and a female bearing A; (2) a male bearing A and a female bearing a; (3) a male bearing a and a female bearing A; and (4) a male bearing a and a female bearing a. That is to say, among each four fertilised eggs that result, there will tend to be 1 AA, 2 Aa, and 1 aa. Seeing that A is invariably dominant, there will in the second generation be three individuals with the dominant to one individual showing the recessive character; of the former, however, two will be heterozygotes, which would exhibit segregation according to the same principle in the ensuing generation, whilst the other, as well as the individuals possessing the recessive character, are *homozygotes* and can be bred true to type.

Further evidence in support of this hypothesis is furnished

by the result of crossing the hybrid of the first generation with one or other parent (i.e. $Aa \times AA$ or $Aa \times aa$). In this instance only two kinds of combinations will be obtained, viz. when the hybrid is crossed with the parent-form having the dominant character, AA and Aa, and there are obviously equal chances for either combination to occur.

The second generation of such a cross does, as a matter of fact, afford individuals half of which are hybrid and half pure. Moreover, when it is recalled that the endosperm of Angiosperms develops as the result of a nuclear fusion (p. 469), it is of interest to note that, if varieties of Maize possessing different types of endosperm (*i.e.* variously coloured or containing sugar and starch respectively) are crossed, the endosperm of the resulting seeds exhibits evidence of its hybrid origin.

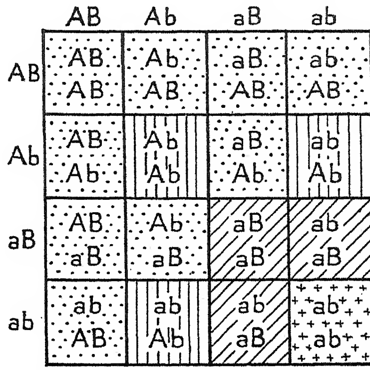

FIG. 413. Scheme to illustrate the progeny of the second generation when two pairs of characters (Aa, Bb) are taken into consideration. The individuals of the first generation will all have the constitution $AaBb$. When segregation occurs, the resulting gametes will have the four possible constitutions AB, Ab, aB, ab[1], and the scheme shows the possible methods of combination of such gametes. When both dominants are present (in nine out of sixteen) the squares are cross-hatched, when the dominant A is present the shading slopes from left to right, when B is present from right to left; when neither dominant occurs the square is left unshaded.

If two pairs of characters are considered, it has been found experimentally that, whilst the first generation consists only of hybrids showing both dominants, the second comprises a number of distinct individuals tending to occur in the following proportions: 9 with both dominant characters, 3 with one dominant and one recessive, 3 with the other dominant and the other recessive, and 1 showing both recessives. The relations will be plain if the diagram in Fig. 413 is studied. Thus, if yellow round Peas are crossed with green angular ones, the first generation all bear yellow round Peas; in the second generation there will be 9 yellow round: 3 yellow angular: 3 green round: 1 green angular. Of the nine individuals showing both dominant characters only one breeds true, as also does the one bearing both recessive characters. The

[1] The combinations Aa and Bb do not arise, since dominant and recessive characters are segregated.

remainder, on being self-fertilised, exhibit segregation according to the particular characters which they contain.

The dominance of a character is only important for the elucidation of the observed facts in the many instances where dominance occurs. But the principle of segregation is equally applicable where the heterozygote is intermediate between the two parents, or, as in some plants, even differs from both. A hybrid intermediate between the two parents is obtained, when the Star and Chinese

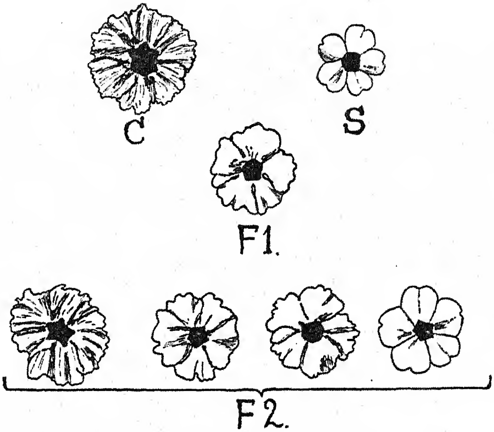

FIG. 414. Hybrids between Chinese (*Primula sinensis*) and Star Primroses (*P. stellata*). At the top the two parents, the Chinese (*C.*) with large, rather wavy, much crenated petals, and the Star (*S.*) with smaller flat petals exhibiting only a notch. The F1 generation is intermediate between the two in these respects. In the F2 segregation takes place in the usual way. (After Punnett.)

Primroses are crossed. The petals in the first generation are intermediate in character between those of the two parents (Fig. 414); in the second generation segregation takes place in the usual way, the hybrid-individuals (one-half) still exhibiting flowers of the intermediate type, whilst the remainder consist of Star and Chinese Primroses in equal numbers.

Hybridisation experiments not only teach us the principle of segregation of characters, but also emphasise the fact that external appearance (phenotypic expression) is no certain guide to internal characteristics (genotypic constitution). This is strikingly illustrated by the effect of crossing particular pure-bred strains of white-flowered Sweet Peas. We should naturally expect all the offspring to be white-flowered too, but in reality all have coloured flowers, with a purple standard and blue wings. Actually one white parent contains the determinant for a colour-producing substance, while the other white parent bears the determinant for

an oxidase, and it is only when both determinants are associated in the same individual that a coloured flower is produced. By breeding plants the limited knowledge obtained by mere examination of the genotypic constitution of any organism, that is, of its hereditary potentialities, can be to some extent supplemented.

When two varieties cross in nature, the appearance of the hybrid is of course influenced by all the characters present in the parents. Whether it resembles one or other parent, or is roughly intermediate between them, will depend on whether one

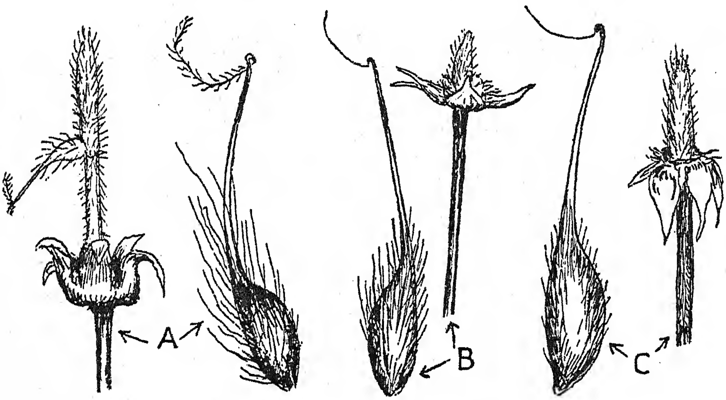

FIG. 415. *Geum rivale* (A), *Geum urbanum* (C), and the hybrid between them, *Geum intermedium* (B). In each the receptacle and calyx are shown, together with an enlargement of a single carpel.

parent contributes a greater proportion of dominant, or more conspicuous, characters than the other. Common examples of such hybrids in the wild state are afforded by various Willows, *Geum intermedium* (Fig. 415, B), *Quercus intermedia*, etc.

Certain characters are commonly inherited together and these are termed *linked characters*. Since the number of such groups of linked characters has in some species been shown to correspond to the number of chromosomes (*e.g.* seven in the Sweet Pea), it is reasonable to assume that the genes belonging to any one linkage-group are located in the same chromosome. Nevertheless, during the intimate association of chromosome-pairs that occurs in meiosis, there would appear to be occasional interchange of parts of chromosomes (*crossing over*, Fig. 412, G), which accounts for the fact that the characters of a particular linkage-group are not invariably inherited together. The persisting points of contact between the chromosomes, viz. the chiasmata, are held to indicate the points at which crossing over has occurred. Thus segregation of parental

characters in hybrid offspring may not be complete and hence hybridisation may bring about a change in the gene complex.

The nuclei of the vegetative cells of the diploid phase would appear to contain equivalent sets of chromosomes from the two parents, so that the number of chromosomes in this phase is ordinarily a multiple of two. In the haploid phase, however, there may often be an odd number of chromosomes. If, then, two species or varieties be crossed, the one with an even, and the other with an odd, haploid number, the hybrid will have an odd number of chromosomes in its diploid nuclei. Such a hybrid is normally sterile, and it is evident that here no balanced separation of chromosomes in meiosis is possible.

Instances are known, however, in which a doubling of the uneven diploid number of chromosomes takes place in such sterile hybrids, resulting in tetraploid plants capable of balanced meiosis and producing fertile seed (e.g. *Primula kewensis*). Even where the diploid number of chromosomes in a hybrid is even, there may be a physiological lack of balance between the two sets leading to sterility.

Replication of chromosomes like that referred to above is known as *polyploidy*,[1] and is not confined to hybrids. The causes leading to this phenomenon are no doubt diverse; one of them is probably a suppression of the reduction division, so that the gametes have the same chromosome-content as the vegetative cells of the parent-plant. Triploids may, *inter alia*, result from the fusion of a diploid gamete with a normal haploid gamete. A few instances are known among Flowering Plants in which the vegetative nuclei of an individual contain the haploid number of chromosomes. Such plants only differ from diploid individuals of the same species in the smaller size of their parts.

In a number of genera (e.g. *Rosa*, *Primula*) that have been investigated the diploid numbers in the diverse species often show various multiples of a basic number (cf. the table below). This suggests that in nature the origin of species within such genera has taken place partly in association with polyploidy. In certain genera (e.g. *Carex*, *Iris*) a very wide range in chromosome-numbers has been established.

[1] See C. D. Darlington, *Chromosomes and Plant Breeding*, Macmillan & Co., 1932 (112 pp.), a clear introductory account; J. B. S. Haldane, *Causes of Evolution*, Longmans, Green & Co., 1932 (235 pp.).

TABLE OF CHROMOSOME NUMBERS.

Rosa spp. 14 (*R. indica*, diploid); 21 (*R. provincialis*, triploid); 28 (*R. gallica*, tetraploid); 35 (*R. canina*, pentaploid); 42 (*R. Moyesii*, hexaploid); 56 (*R. hilliana*, octoploid).

Iris spp. (Haploid numbers), 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 36, 41–42, 42, 43–44, 54–56.

Primula spp. 16 (*e.g.* Sections *Stenocalyx* and *Souliei*); 18 (*Verticillatæ*, *Malacoides*); 20 and 22 (most frequent); 24 (*Septemlobæ* and *Bullatæ*); 36, 40, 44, 54, 72, 126.

Fragaria spp. 14 (*F. vesca*, diploid); 42 (*F. elatior*, hexaploid); 56 (*F. virginiana*, octoploid); 56 also in *F. chilœnsis* and the Garden Strawberry.

Prunus spp. 16 (*P. persica*, *P. avium*); 32 (*P. cerasus*, *P. spinosa*); 48 (*P. domestica*, *P. malaheb*).

It has long been familiar to gardeners that shoots, which show a mingling of the characters of scion and stock, are sometimes produced as a result of grafting (p. 252), and for some time these were thought to be of a hybrid character. The intermediate nature of these so-called *graft-hybrids* or *chimæras* appears to be due to the fact that both scion and stock contribute to their development, the tissues of the one forming a skin over those of the other. These are spoken of as periclinal chimæras. The character of the seeds, and of the resulting offspring, is determined by the plant responsible for the formation of the subepidermal layer from which the archesporial tissue (pp. 437, 445) arises. This explains the fact that the seeds of graft-hybrids always breed true to the characters of either the scion or the stock. The commonest example of such a chimæra is that known as *Cytisus adami*, which is due to the grafting of the Purple Broom (*Cytisus purpureus*) on the Laburnum (*C. laburnum*). Other types of chimæras are known in which the tissues are not distributed in this regular manner. It should be added that the mode of origin of many chimæras (*e.g.* zonal *Pelargonium*) is not known.[1]

Sexual fusion may be regarded as operating in two ways, firstly as a stimulus leading to further development, secondly as a possible means of introducing new characters or of rearranging those already present in the two parents. The former result may be attained by other stimuli. Amongst animals, for instance, the eggs of the Frog have been caused to develop by mere pricking with a glass needle covered with blood-serum, whilst among plants eggs of *Fucus* have been stimulated to divide by treatment with solutions having a higher osmotic pressure than sea-water. The polyembryonic seeds of the Orange (cf. p. 473) furnish an analogous example; here certain cells, apart from the fertilised egg, have developed into

[1] For further details, see W. Neilson Jones, *Plant Chimæras and Graft Hybrids*. Methuen & Co., 1934 (136 pp.).

embryos, but there is no evidence that the apogamously produced seedlings are any less vigorous than those resulting from sexual fusion. It seems probable, therefore, that the chief advantage of sexual reproduction lies in the possibility of producing organisms, with a slightly different genotypic constitution, such as may survive under conditions that would be unfavourable to the pure parent strain. In other words, sexual reproduction provides material upon which natural selection can operate.

In *vegetative propagation* the offspring normally exhibit no change of character, as compared with the parent, and new forms can only arise by mutation. Mutations in vegetatively produced offspring, and even in certain branches of an individual, have indeed been occasionally observed (cf. p. 586), and may be the means of maintaining the race in harmony with its environment. Although vegetative mutation appears to be comparatively infrequent, it should be borne in mind that groups like Bacteria and Cyanophyceæ, which multiply exclusively by vegetative means, often do so with great rapidity. An exceptionally large number of generations is therefore formed in a short time, and so presumably the opportunities for mutation are proportionately increased.

The *theory of evolution* interprets the resemblances between the members of a genus or family (cf. pp. 277, 605) as the necessary consequence of their origin from a common ancestor or from closely related forms. It has already been seen how new types can arise as an outcome of mutation, hybridisation, etc. Since these show a great resemblance to their known parents, it is reasonable to regard the many features in common, between the species of a genus or between the genera of a family, as indications of a natural affinity between them. This is strikingly portrayed in certain families which have marked physiognomic characteristics, as, for example, the succulent Crassulaceæ and Cactaceæ, the essentially aquatic Potamogetonaceæ, and the completely parasitic Orobanchaceæ.

What has already been said, then, with regard to the distribution of species (p. 570) should also apply in a general way to genera and families, if these really comprise groups of forms with natural affinities. In many, indeed, the same principles are applicable; for example, the genus *Commidendron* (a member of the Compositæ), with three species, is restricted to St. Helena, and whole families are sometimes largely confined to definite areas, as the Epacridaceæ (which are closely allied to the Ericaceæ) to Australia and Tasmania.

Geological research has shown that oceans and continents have undergone manifold changes in area and level, even during the period of existence of many living species. These secular changes

probably afford the clue to the *discontinuous distribution* of many species and families. Certain groups, now represented only in widely separated areas over the earth's surface (*e.g.* the Cycads, Fig. 416), are known to be ancient, and may well have attained their wide distribution before the present barriers were as pronounced or had even become established. A similar instance is furnished by the occurrence of the same arctic species (p. 575) on the tops of many high mountains, although the present-day climate of the plains offers an insurmountable barrier to their dispersal from one chain to the other.

The conception of evolution regards the organic world, as we find it to-day, as consisting not of a number of immutable forms, but as presenting one phase in an ever-changing series. The organisms of the present are the offspring of those of the past, and will themselves, in turn, give rise to the organisms of the future. Those animals or plants which have become extinct must be supposed to have failed to "make good" in the competitive struggle. From the fossil records it is known that whole floras and faunas have thus perished, leaving no living representatives or only much modified descendants (cf. Chapters XXXII, XXXIII). Such disappearance may well be an outcome of the secular, but none the less profound, changes that have marked the history of the earth's surface since life first appeared. Organisms, unsuited to the new conditions, would inevitably perish as a result of being handicapped in competition against, either their more adaptable contemporaries, or new forms which were better equipped to withstand the changed environment.

The evolutionist conceives of all life as having developed from relatively simple undifferentiated unicellular organisms, many of whose descendants, through the ages, have gradually acquired an increasing complexity of structure in relation to progressive division of labour. On this hypothesis, if our knowledge of all the extinct plants of former eras were complete, we could reconstruct the genealogical history (*phylogeny*) of the present-day forms. Those of the past would furnish the links connecting genus with genus, and family with family, till all were connected up to the primitive simple organisms from which they sprang when life first developed. The fact that many fossil plants and animals do combine characters, that now serve to distinguish separate groups, is one of the strongest pieces of evidence for such a conception. But, further, the geographical distribution of living plants and animals, showing, as already noted, restriction of similar species to definite areas, is most readily explained as due to their origin, in that area, from common or closely related parents. But the origin of species by hybridisation

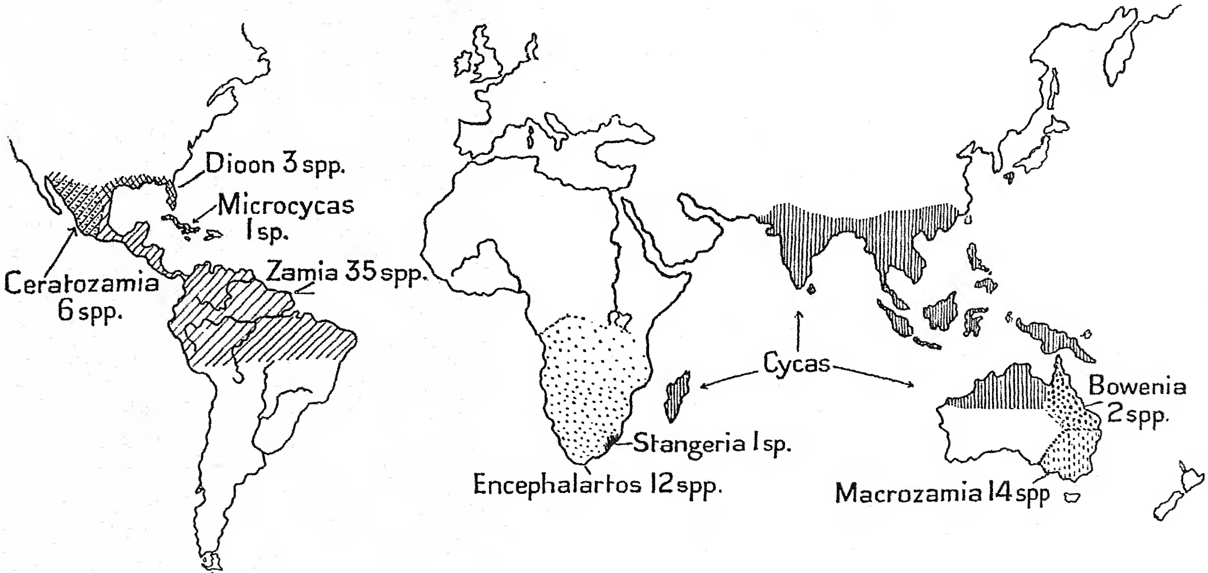

FIG. 416. Map of world showing present-day distribution of the genera of Cycadales.

indicates that the old concept of a genealogical tree is too simple, ignoring as it does the numerous cross-connections between the ever-increasing complexity of the branch-system.

The features characteristic of the various members of a genus or family are often only fully apparent in the adult state, whilst the earlier the stage of development of an organism, the more difficult does the determination of its identity become. The history of the individual may be regarded as, to a very limited extent, recapitulating the history of the race; in this connection it may be noted that in the ordinary course of reproduction every individual commences life as a single cell. Such an interpretation also explains the frequent occurrence of rudimentary structures (*e.g.* the gill-slits in the embryo of the Chick, or the pinnate leaves in the seedling stages of species of *Acacia* possessing phyllodes, Fig. 417), which often perform no function, or are even completely lost, in the adult. Even amongst living organisms a graduated series, as has been seen in Chapters XXV to XXXVII, can be recognised. The simplest members of this series are doubtless relics, though almost certainly modified, of the earliest flora which have found a place in the economy of nature even under existing conditions.

The highest efficiency is only attained by great specialisation which proportionately diminishes the capacity for adaptation to a new environment. But the world of living things is a world of never-ceasing change, and hence the past history of the organic universe is the history of extinction of specialised races and individuals. The future of a group is thus seen to be dependent upon its less specialised, and thus at the moment less successful, members. But as in time, so too in space, the spread of a species may be handicapped by its lack of plasticity.

The brief review of the groups which we have given is sufficient to indicate that the extinct Clubmosses and Horsetails, in the era of their success, were more specialised and more complex than their present descendants, which play so subordinate a rôle, and probably owe their survival to features which characterised the less successful members of these groups in the past. Such considerations lead one to suspect that the subordinate groups and individuals of any one age are the most likely starting-points for the dominant vegetation of the next, and so we can understand why the fossil record presents us with abundant examples of clearly defined groups (*i.e.* of the prevalent successful forms) and comparatively few representatives of groups "in the making." Indeed, the fossil plants of past ages and the living organisms of to-day combine to emphasise the rarity of the "missing link" which,

like the thinker in advance of his age, is not sufficiently in harmony with the environment to command success, but yet marks the

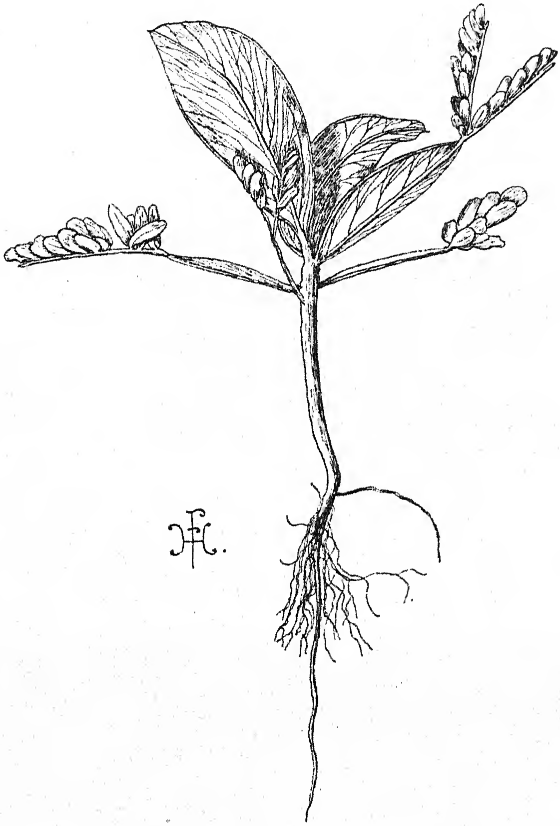

FIG. 417. Seedling of an *Acacia*, showing the gradual differentiation of phyllodes, and suppression of the laminæ, in leaves of successive ages.

beginnings of the facies of the future. It is not, therefore, surprising that our progress in the reconstruction of the genealogical tree of the Vegetable Kingdom is slow, and that many of the groups remain in striking isolation from one another.

CHAPTER XLVIII

CLASSIFICATION OF BRITISH FLOWERING PLANTS

CLASSIFICATION of plants [1] is necessary in order to provide a general view of the immense diversity of forms. Moreover, since plants are classed on the basis of all their characteristics, classification aims at placing similar plants near together and dissimilar ones more or less far apart, so that the more perfect it becomes, the more completely does it afford an expression of the relationships between the different forms. Any classification is, however, necessarily arbitrary because it cannot indicate cross-connections and because it presents in two dimensions only what is really a three-dimensional complex. The following epitome of the main groups of the Vegetable Kingdom includes those already described in Chapters XXV to XXXVII, but also adds some others less familiar in order to give a more complete picture of the range of plant-form involved.

1. Thallophyta.

   Algæ.

   (*a*) Cyanophyceæ or Myxophyceæ (Blue-green Algæ).
   (*b*) Chlorophyceæ (Green Algæ).
   (*c*) Xanthophyceæ or Heterokontæ (Yellow-green Algæ).
   (*d*) Chrysophyceæ (Orange-yellow Algæ, include many motile species).
   (*e*) Bacillarieæ (Diatoms).
   (*f*) Dinophyceæ or Peridinieæ (mainly motile organisms of fresh or salt water).
   (*g*) Phæophyceæ (Brown Algæ).
   (*h*) Rhodophyceæ (Red Algæ).

   Charophyta (Stoneworts).

   Myxomycetes (Slime Fungi).

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[1] Valuable reference-books are: J. C. Willis, *A Dictionary of Flowering Plants and Ferns*, Cambridge Univ. Press, 6th edit., 1931 (752 pp.); J. Lindley and T. Moore, *The Treasury of Botany*, 2 vols., London, 1884, which contains much miscellaneous information about the higher plants; and A. B. Rendle, *The Classification of Flowering Plants*, 2 vols., Cambridge Univ. Press, 1925. A. S. Hitchcock, *Methods of Descriptive Systematic Botany*, T. Wiley, New York, 1925 (216 pp.), explains the terminology, conventions, and technique of floristic botany. Floras are listed on p. 578.

Bacteria.
Fungi.

- (*a*) Phycomycetes { Zygomycetes (incl. *Mucor*). / Oomycetes (incl. *Pythium*).
- (*b*) Basidiomycetes.
  - (1) Uredineæ (Rust Fungi).
  - (2) Ustilagineæ (Smuts and Bunt).
  - (3) Eubasidii { Hymenomycetes (Toadstools and Mushrooms). / Gasteromycetes (Puff-balls, Stinkhorn, etc.).
- (*c*) Ascomycetes { Plectomycetes (incl. *Eurotium*). / Discomycetes (incl. *Peziza*, etc.). / Pyrenomycetes (*Claviceps*, etc.).
- (*d*) Lichenes (Fungi symbiotic with algæ).

2. Archegoniatæ.

A. Bryophyta.

- (*a*) Hepaticæ (Liverworts).
  - (1) Marchantiales (incl. *Fegatella*, *Marchantia*, etc.).
  - (2) Jungermanniales (incl. *Cephalozia*, *Pellia*, etc.).
  - (3) Anthocerotales.
- (*b*) Musci (Mosses).
  - (1) Sphagnales (Bog-mosses).
  - (2) Andreæales.
  - (3) Bryales (incl. most of the Mosses).

B. Pteridophyta.

- Filicales (Ferns).
- Psilophytales (Fossil).
- Psilotales (*Psilotum* and *Tmesipteris*).
- Sphenophyllales (Fossil).
- Equisetales (Horsetail "Ferns" and Fossil Calamites).
- Lycopodiales (incl. *Lycopodium*, *Selaginella*, *Lepidodendron* (Fossil), and *Isoetes*).

3. Spermaphyta.

1. Pteridospermæ (*Lyginopteris*, Fossil only).
2. Gymnospermæ.
   - Cycadales.
   - Bennettitales (Fossil only).
   - Cordaitales (Fossil only).
   - Ginkgoales (Maidenhair Tree, *Ginkgo*).
   - Coniferales (*Pinus*, *Taxus*, etc.).
   - Gnetales.
3. Angiospermæ.
   - Monocotyledones (incl. Liliaceæ, Gramineæ, etc.).
   - Dicotyledones.
     - (*a*) Archichlamydeæ or Polypetalæ (Ranunculaceæ, Leguminosæ, etc.).
     - (*b*) Sympetalæ (Primulaceæ, Scrophulariaceæ, etc., an artificial assemblage of the more specialised families).

The rest of this chapter is devoted to a very brief summary of some of the salient characteristics of the families of Angiosperms most commonly represented in the British flora. In the taxonomy of Flowering Plants, as in that of other classes (p. 277), the constituent members are placed in various aggregates resembling one another in an increasingly greater number of features.

Thus, certain forms are classed together as *species*, such as the different strains of *Capsella bursa pastoris* (Fig. 3) or the different habitat-forms of *Gnaphalium uliginosum* (Fig. 407). The individuals differ only in few or less important details, such as size, shape of leaves, presence or absence of hairs, time of flowering, etc. Within the species are included *varieties* which differ in a few heritable characters and *ecads* or *forms* which show non-heritable differences imposed by habitat-conditions.

Different species are grouped together in a wider aggregate, the *genus*, as, for example, the diverse species of *Ranunculus*; all the species of such a genus resemble one another in certain important characters, but differ in more numerous and more significant respects than the individuals of the same species. For instance, in *Ranunculus* all the species agree in having flowers with a calyx and corolla, nectary-bearing petals, numerous stamens, a fruit composed of a collection of achenes, etc. The individual species, on the other hand, differ in habit, in the shape and degree of lobing of the leaves, the size and colour of the petals, the form of the peduncle, and the character of the pericarp, as well as in many other smaller points. *Ranunculus*, together with other genera such as *Clematis*, *Anemone*, *Caltha*, *Helleborus*, *Aquilegia*, *Aconitum*, *Delphinium*, etc., are comprised in the *family* Ranunculaceæ, all of them being distinguished by possessing leaves with sheathing bases, a hypogynous flower, numerous stamens, an apocarpous ovary, and fruits usually consisting of achenes or follicles. It is a convention justified by experience that the characters of the reproductive organs are used to distinguish genera and aggregates of higher order, whilst characters of the vegetative organs serve more particularly to identify species. Related families are grouped together into *cohorts*. Thus Ranunculaceæ, Nymphæaceæ, Berberidaceæ, etc., belong to the cohort Ranales.

All the species of a given genus are in scientific usage designated by a common Latin name, all the Buttercups being species of the genus *Ranunculus*. The species are distinguished by a second Latin word placed after that denoting the genus; thus, the Meadow Buttercup is known as *Ranunculus acris*, whilst the Field Buttercup is *Ranunculus arvensis*. The letter L (for Linnæus) or other

abbreviation following a Latin binomial indicates the botanist by whom the species was first properly described.

In describing the following families we shall frequently employ a *floral formula* to indicate the usual number of parts in the successive whorls. The number of members in each is represented by a numeral and, where there is more than one whorl of the same kind, the numbers for each whorl are joined by a + sign. The calyx is represented by K, the corolla by C, a perianth by P, the stamens by A, and the ovary by G. The joining together of members of a whorl is indicated by putting the corresponding numeral in brackets, whilst a line above or below the numeral representing the ovary marks the inferior or superior position of the latter. Apart from this, the following abbreviations are employed: *alt.*, alternate; *anem.*, anemophilous; *apocarp.*, apocarpous; C, corolla; *cpd.*, compound; *cpl.*, carpel; *end.*, endosperm present; *end. O*, endosperm absent; *entom.*, entomophilous; *epig.*, epigynous; *exstip.*, exstipulate; *flr.*, flower; *hypog.*, hypogynous; *inf.*, inferior; *infl.*, inflorescence; *irreg.*, irregular; K, calyx; *opp.*, opposite; *ov.*, ovary; *perig.*, perigynous; *plac.*, placenta; *protandr.*, protandrous; *protog.*, protogynous; *reg.*, regular; *sp.*, species; *sta.*, stamen; *stip.*, stipulate; *sup.*, superior; *syncarp.*, syncarpous; *unisex.*, unisexual; ♂, male; ♀, female; ☿, hermaphrodite; ∞, numerous.

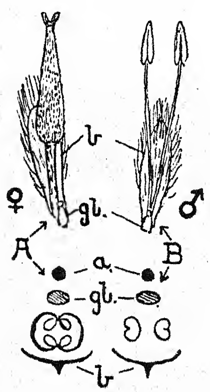

FIG. 418. Structure of flowers of *Salix caprea* (enlarged). The ♂ and ♀ flowers above and the corresponding floral diagrams below. *a*, axis of catkin; *b*, bracts; *gl.*, honey-glands.

A. DICOTYLEDONS

(*a*) ARCHICHLAMYDEÆ (Families 1–17)

Perianth, when present, usually with free parts

1. SALICACEÆ (SALICALES)

Trees and shrubs with alt. stip. leaves, the stipules often caducous. Infl. a catkin. Flrs. diœcious, unisex., hypog., naked. ♂ flrs. (Fig. 418, ♂) with 2–∞ sta., anthers often brightly coloured. ♀ flrs. (Fig. 418, ♀), ov. sup., bicarpellary, unilocular, with two parietal placs. bearing ∞ ovules; stigma bilobed. Small nectary (Fig. 418, *gl.*) or its equivalent in both flrs. Fruit a capsule, seeds bearing tufts of hairs, end. O. Entom. or anem.

The British genera are:—*Salix* (Willow, Fig. 418), with 2–5 sta. in the ♂ flrs., and a one- or two-toothed nectary, entom.; *Populus* (Poplar), with ∞ sta. and a cup-shaped structure analogous to the nectary of *Salix*, anem.

2, 3. BETULACEÆ AND FAGACEÆ (FAGALES)

Trees and shrubs, with almost naked flrs., the ♂ in definite catkins. The Betulaceæ (Fig. 419, C–F) have partial infl. which are reduced dichasial cymes subtended by an involucre of fused bracts; the ♀ flrs. of 2 cpls., ov. biloc. inf., with one pendulous ovule in each loc., ♂ with 2–10 sta. (Fig. 419, F). Chief genera: *Corylus* (Hazel, Fig. 314); *Betula* (Birch, Fig. 419, E); *Carpinus* (Hornbeam, Fig. 419, C and D); and *Alnus* (Alder, Fig. 419, F).

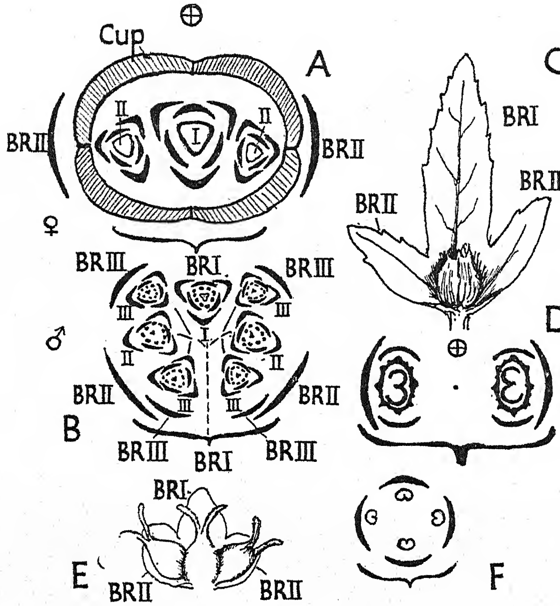

FIG. 419. Betulaceæ and Fagaceæ. A, Floral diagram of female, and B, Floral diagram of male partial inflorescence of *Castanea vulgaris*. Both are reduced dichasia, the successive flowers being numbered in order of development: I, II, III. C, Female flowers and subtending bracts of *Carpinus betulus*, in fruiting stage. D, Floral diagram of same. E, Group of three female flowers of *Betula*. F, Floral diagram of male flower of *Alnus*. BR. I . . . BR. III, bracts of successive flowers; BR. II is bract of the second flower and bracteole of the first.

The Fagaceæ (Fig. 419, A and B) have still more reduced dichasial infl., the ♀ flrs. of 3 cpls. being contained in a cupule (p. 474); ov. triloc. (p. 477) inf., with 2 ovules in each loc. Fruit a one-seeded nut. Chief genera: *Quercus* (Oak, Fig. 362), with cup-like cupule; *Fagus* (Beech) and *Castanea* (Sweet Chestnut), both with prickly cupules.

4. URTICACEÆ (URTICALES)

Herbs with alt. or opp. stip. leaves, often with stinging hairs (p. 160). Flrs. unisex. (Fig. 420); P inconspicuous, of 4–5 members; sta. 4–5, opp. P; ov. bicarp., uniloc., 1 orthotropous ovule; anem. Fruit an achene.

British genera: *Urtica* (Stinging Nettle, Fig. 420, A and B); *Parietaria* (Pellitory, Fig. 420, C). *Humulus* (Hop, Fig. 10) belongs to the allied Moraceæ, which also include Fig and Mulberry.

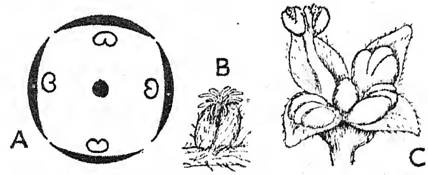

FIG. 420. Urticaceæ. A, Floral diagram of male flower, and B, side-view of female flower of *Urtica*. C, Male flower of *Parietaria*, showing stamens opposite perianth segments.

5. POLYGONACEÆ (POLYGONALES)

Herbs, with alt. leaves with ochrea (Fig. 74, E). Infl. usually spike-like. Flrs. (Fig. 421) inconspicuous; P 3 + 3 in *Rumex* (Dock, Fig. 421, A), 5 in

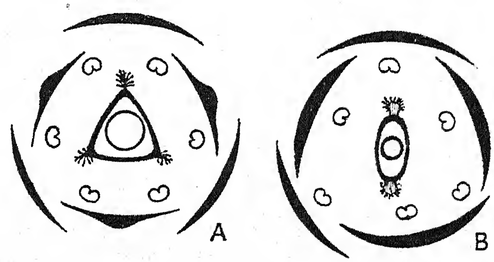

FIG. 421. Polygonaceæ. Floral diagrams of *Rumex* (A) and *Polygonum* (B).

Polygonum (Knotweed, Fig. 421, B), 2 + 2 in *Oxyria*; A 5–8; G (3–2), ov. sup., uniloc., one basal orthotropous ovule. Fruit a trigonous or biconvex achene, P persistent.

To this family belong *Rheum* (Rhubarb) and *Fagopyrum* (Buckwheat).

6. CHENOPODIACEÆ (CENTROSPERMÆ)

Herbs with exstip. leaves and small flrs., unisex. or ☿, often halophytes (p. 566). P 3–5; sta. usually 3–5; G 2, ov. uniloc. with one campylotropous ovule. Fruit an achene.

British genera: *Atriplex* (flrs. unisex.); *Beta* (Beetroot, ov. half-inf.); *Chenopodium* (Goosefoot); *Obione*; *Salicornia* (succulent halophytes, Fig. 400, with embedded ☿ flrs., A 1–2); *Salsola* (p. 510, solitary axillary flrs.); *Suæda*.

7. CARYOPHYLLACEÆ (CENTROSPERMÆ)

Annual or perennial herbs with opp., often exstip., entire leaves and swollen nodes, mostly glabrous. Infl. mostly a dichasial cyme (Fig. 290, H). Flrs. reg., mostly ☿ (sometimes unisex. in *Lychnis*), hypog., usually with K5 C5 A5 + 5 G(3 to 5) (Fig. 422, C). K poly- or gamosepalous; petals free, often

divided (Fig. 422, A, B) or clawed, sometimes with a corona (*Lychnis*), or absent; sta. in 2 whorls, mostly 10, sometimes 8, often of two lengths; ov. sup. syncarp., of 2–5 cpls., when 5 cpls. either opp. the petals or sepals, with a free central plac., usually bearing ∞ ovules (Fig. 422, E). Stigma with as many lobes as there are cpls. Honey formed at base of sta. (Fig. 315, C). Fruit usually a capsule opening by apical teeth (Fig. 333, *f*), an achene in *Scleranthus*; seeds end. Mostly entom., commonly protandr. Non-poisonous.

The family is subdivided into:

(i) *Alsineæ*:—Calyx polysepalous; flrs. open and shallow (Fig. 422, A). The British genera are: *Arenaria*, with *A. peploides*, a maritime succulent; *Cerastium* (Mouse-ear Chickweed), petals notched, leaves hairy; *Sagina* (Pearlwort), some sp. apetalous and self-pollinated; *Scleranthus*, with stipules, flrs. apetalous and self-pollinated, with only 1 ovule, a common weed of cornfields; *Spergula* (Field Spurrey), a weed with stip. and dwarf-shoots (Fig. 69); *Spergularia*, maritime, with stip. leaves; *Stellaria* (Stitchwort), petals deeply cleft (Fig. 422, A).

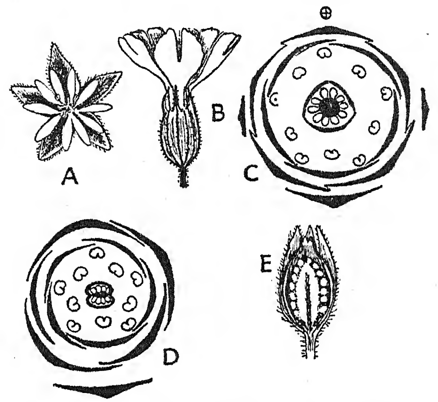

FIG. 422. Caryophyllaceæ. A, Flower of *Stellaria media* (Chickweed), showing open type. B, Flower of *Lychnis*, showing tubular type. C, Floral diagram of *Silene*. D, Floral diagram of *Dianthus*. E, Longitudinal section of fruit of *Lychnis*, showing free central placentation.

(ii) *Sileneæ*:—Calyx gamosepalous; petals clawed; tubular flrs. (Fig. 422, B). The chief British genera are: *Agrostemma* (Corncockle), a weed of cornfields; *Dianthus* (Pink), with only 2 styles (Fig. 422, D); *Lychnis* (Campion, Fig. 422, B), with a well-marked corona (p. 435); *Silene* (Bladder Campion), often with an inflated K (Fig. 435, C).

8. RANUNCULACEÆ (RANALES)

Mostly perennial herbs with alt. (except *Clematis*), occasionally stip. leaves, often deeply palmately lobed and having sheathing bases; stem a root-stock or rhizome with fibrous roots and often bearing radical leaves. Infl. usually cymose, but sometimes a raceme (*Delphinium, Aconitum*) or a single terminal flr. (*Anemone*). Flrs. mostly reg., ☿, hypog., all parts free, commonly with A ∞ G ∞ (Fig. 423). Perianth either consists of K and C (*Ranunculus*, Fig. 293, A) or of one or more petaloid whorls; sta. ∞, often extrorse, mostly spiral; ov. apocarp., sup. Nectaries of various shapes, between sta. and perianth. Fruit a collection of achenes or follicles (capsule in *Nigella*, berry in *Actæa*); seeds end. Mostly entom. and often protandr. An acrid juice (sometimes poisonous) often present.

The family is subdivided into:

(i) *Anemoneæ* (with achenes): The chief British genera are: *Anemone*, involucre of 3 bracteoles, achenes often with aborted ovules; *Clematis*, a woody

climber with opp. leaves, pollen-flrs., and feathery styles (Fig. 337, F); *Ranunculus* (Fig. 423), incl. yellow-flowered sp. and the white-flowered Water Buttercups (Fig. 386), with definite stipules; *Thalictrum* (Meadow-rue), with stip. leaves, a small deciduous perianth, and with pollen-flowers or anem.

(ii) *Helleboreæ* (with follicles):—The chief British genera are: *Aconitum* (Monkshood), with irreg. flrs. and reduced petals, two of which form nectaries beneath the hood (Fig. 324); *Actæa* (Baneberry), with a berry of 1 cpl.; *Aquilegia* (Columbine), with 2 perianth-whorls, each of the inner members being produced into a spur; *Caltha* (Marsh Marigold), nectar at base of cpls.; *Delphinium* (Larkspur), irreg. flr. having a single spur into which two nectary-bearing processes from the petals project (p. 453); *Eranthis* (Winter Aconite) (Fig. 296); *Helleborus* (Christmas Rose), with a persistent perianth-whorl, often green, and trumpet-shaped nectaries (Fig. 315, D); *Trollius* (Globe-flower), with perianth completely covering flr. which is usually self-pollinated.

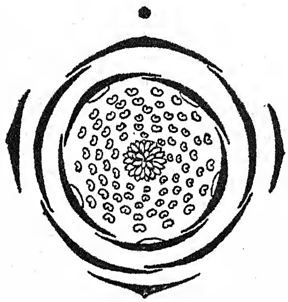

FIG. 423. Floral diagram of *Ranunculus*.

Belonging to the same cohort Ranales are two other British families. The NYMPHÆACEÆ are aquatic perennials, with thick rhizomes and floating leaves (Fig. 379), K 4–5, C and A ∞ and spiral, G 10–20, fruit a capsule with projecting parietal plac. and ∞ ovules. British genera: *Nuphar* (Yellow Water Lily); *Nymphæa* (White Water Lily).

The BERBERIDACEÆ have only one British representative (*Berberis vulgaris*), and are mostly shrubs with usually trimerous (p. 266) flrs. (dimerous in the cultivated *Epimedium*); sta. dehiscing by valves; ov. of 1 cpl. with 1 ovule; fruit a berry.

9. CRUCIFERÆ (RHŒADALES)

Annual or perennial herbs with alt. exstip. leaves, often bearing branched hairs; leaves simple or more or less pinnately lobed (Fig. 3), often radical; roots occasionally tuberous. Infl. a raceme *without bracts*, often corymbose at first. Flrs. usually white or yellow, reg., ⚥, hypog., all parts except cpls. free, usually with K2 + 2 C4 A2 + 4 G(2) (Fig. 424). Calyx of 2 outer median and 2 inner lateral sepals, often upright; petals often clawed and alternating with the 4 sepals; sta. 2 short and 4 long (tetradynamous) or rarely 4 or 2 (Fig. 424, F, G); ov. syncarp., bicarp., with a septum and 2 parietal placs., sup. (D). Stigma usually bilobed (B). Nectaries at base of 2 short sta. (A), the nectar collecting in pouches formed by the lateral sepals (Fig. 317). Fruit a siliqua (Fig. 333, *d*) or silicula (Fig. 4, B); seeds end. O., with a curved embryo. Mostly entom. and protandr. Non-poisonous.

Important British genera with siliquas are: *Arabis*; *Barbarea*, occasionally with bracts to infl.; *Brassica* (Charlock), including Cabbage, Cauliflower, Kohlrabi, Mustard, Turnip, Brussels Sprouts; *Cardamine* (Milkmaid), often with explosive fruits (p. 480); *Cheiranthus* (Wallflower, Fig. 424, A–D); *Dentaria* (Coral-root), with bulbils (p. 234); *Matthiola* (Stock); *Nasturtium* (Water-cress); *Sisymbrium* (incl. Hedge Mustard).

Genera with siliculas include: *Capsella*; *Cochlearia* (Scurvy Grass, Horse-radish); *Erophila* (Whitlow-grass); *Iberis* (Candytuft) (Fig. 316); *Lepidium*

(Cress, Fig. 424, F); *Subularia* (Awlwort), a submerged aquatic with cylindrical leaves.

Genera with indehiscent fruits are: *Cakile* (Sea Rocket), with lomentum; *Crambe* (Sea-kale), maritime, with fleshy leaves and a spherical fruit; *Isatis* (Woad), employed in dyeing; *Raphanus* (Radish), with a lomentum; *Senebiera* (Wart-cress), a common weed with two-seeded fruits.

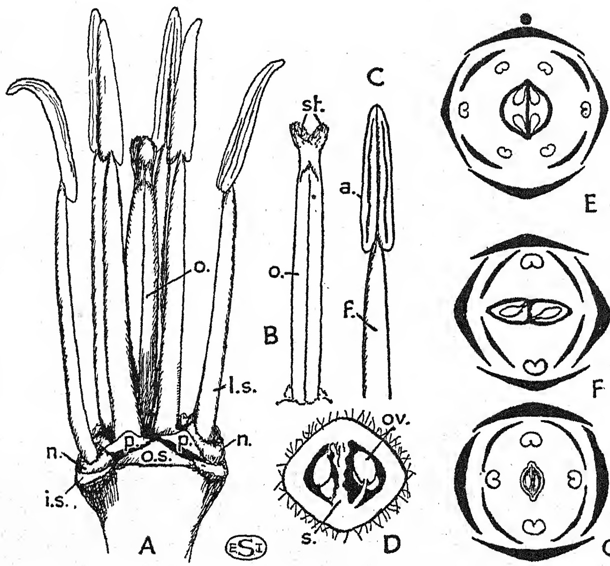

FIG. 424. Cruciferæ. A, Flower of *Cheiranthus* with sepals and petals removed. *l.s.*, lateral stamens; *n.*, nectary; *o.*, ovary; *o.s.* and *i.s.*, scars of outer and inner sepals; *p.*, petal scars. B, Ovary (*o.*) bearing two stigmas (*st.*). C, A single stamen showing filament (*f.*) and anther (*a.*) dehiscing. D, Transverse section of ovary showing ovules (*Ov.*) and septum (*s.*). E, Floral diagram of *Cheiranthus*. F, Floral diagram of *Lepidium virginianum*. G, Floral diagram of *Cardamine hirsuta*.

10. PAPAVERACEÆ (RHŒADALES)

Mostly herbs with alt. leaves and latex (p. 94). Flrs. reg., K2 caducous, C2 + 2, A∞, G($\underline{2-\infty}$), ov. syncarp. uniloc. with parietal plac. and ∞ ovules. Fruit a capsule (Fig. 333, *h*).

The British genera are: *Chelidonium* (Greater Celandine) and *Glaucium* (Horned Poppy), with yellow latex, pod-like fruits of 2 cpls., the latter with a septum as in Cruciferæ; *Meconopsis* (Welsh Poppy), with 5–6 cpls., and *Papaver* (Poppy), with 4–20 cpls., have capsular fruits (Fig. 333, *h*).

The closely allied FUMARIACEÆ are devoid of latex and have irreg. flrs. with K2, C4, A of two tripartite stamens, G($\underline{2}$). Fruit one-seeded.

11. ROSACEÆ (ROSALES)

Perennial herbs (*Alchemilla arvensis* is an annual), shrubs, or trees, with alt., often stip. leaves which are simple or compound. Infl. cymose or racemose. Flrs. reg., mostly ☿, hypog. or epig. or most commonly perig., all parts generally

free, usually with K5 C5 A5 + 5 + 5 + . . . (few in certain genera), G∞. Calyx occasionally with an epicalyx (Fig. 297, D); ov. usually apocarp. and sup. (syncarp. and inf. in *Pyrus*). Receptacle more or less hollowed out (Fig. 292, B, C). Honey formed on receptacle between sta. and cpls. Fruit various, a drupe or an aggregate of drupes or achenes; false fruits (Fig. 336, C–E) in certain genera. Mostly entom. and often protandr.

The following subdivisions of the family are British:—

(i) *Spiræoideæ*:—Relatively few whorled follicles borne on a small central protuberance of the but slightly concave receptacle. Many sp. of *Spiræa* are cultivated shrubs.

(ii) *Pomoideæ*:—Shrubs or trees, with an inf. syncarp. ov.; generally a false fruit. British genera are: *Cratægus* (Hawthorn); *Pyrus* (Apple, Fig. 292, A; 336, E, Pear, Medlar); and *Sorbus* (Mountain Ash).

(iii) *Rosoideæ*:—Shrubs and herbs, with apocarp., perig. flrs. and a more or less deeply hollowed receptacle (Fig. 292, B and C). The most important genera are: *Agrimonia* (Agrimony), with cup-shaped receptacle bearing hooks (Fig. 339, A), ov. of 1 or 2 cpls.; *Alchemilla* (Lady's Mantle), apetalous tetramerous flrs., with cup-shaped receptacle, few cpls., Fly-pollinated; *Fragaria* (Strawberry), with epicalyx; *Geum*, with epicalyx (Fig. 297, D) and fruit of hooked schenes (Fig. 339, D); *Potentilla* (Cinquefoil, Tormentil, Fig. 426, C); *Poterium* (Salad Burnet), apetalous unisex. tetramerous flrs. with branched stigmas, fruit of 1–3 achenes, anem.; *Rosa* (Fig. 336, C); *Rubus* (Blackberry, Raspberry), fruit of a number of drupes (Fig. 335, G and H); *Ulmaria* (Meadowsweet).

(iv) *Prunoideæ*:—Trees, with a single cpl. in a concave receptacle; fruit a drupe (Fig. 335, E and F); *Prunus* (Almond, Apricot, Cherry, Plum, Sloe).

12. SAXIFRAGACEÆ (ROSALES)

Herbs or shrubs, with perig. or epig. flrs., K5 C5 A5 or 5 + 5, G2 (Fig. 425, A–C); ov. uniloc. with parietal plac. or bilocular with axile plac., loculi often separate above; often markedly protandr. Fruit a capsule or berry.

The British genera are: *Chrysosplenium* (Golden Saxifrage), apetalous marsh-plants; *Parnassia* (Grass of Parnassus), with 5 sta., branched staminodes and 3–4 cpls.; *Ribes* (Currant, Gooseberry), fruit a berry (Fig. 335, A, B, and Fig. 425, B); *Saxifraga* (Fig. 425, A and C), leaves often with chalk-glands (p. 197; Fig. 197, C), fruit a capsule, many alpines.

13. CRASSULACEÆ (ROSALES)

Mostly succulent herbs, with alt. leaves and usually cymose infl.; K4–12 C4–12 A8–24 G usually $\underline{5}$, apocarp. (Fig. 425, D). Fruit a collection of follicles.

The chief British genera are: *Cotyledon* (Wall Pennywort), C gamopetalous, with a corm; *Sedum* (Stonecrop, Fig. 357, A, C; 425, D).

14. LEGUMINOSÆ (ROSALES)

Annual or perennial herbs, shrubs, or trees, with alt. stip. leaves, usually cpd. and pinnate, leaflets entire, frequently modified into tendrils; roots with root-nodules (p. 219 and Fig. 133). Infl. racemose. Flrs. irreg., ☿, slightly perig., usually with K(5) C5 A(5 + 5) G$\underline{1}$ (Fig. 426, A). K more or less gamosepalous, frequently two-lipped (Fig. 320, A), odd sepal anterior (Fig. 426, A, B);

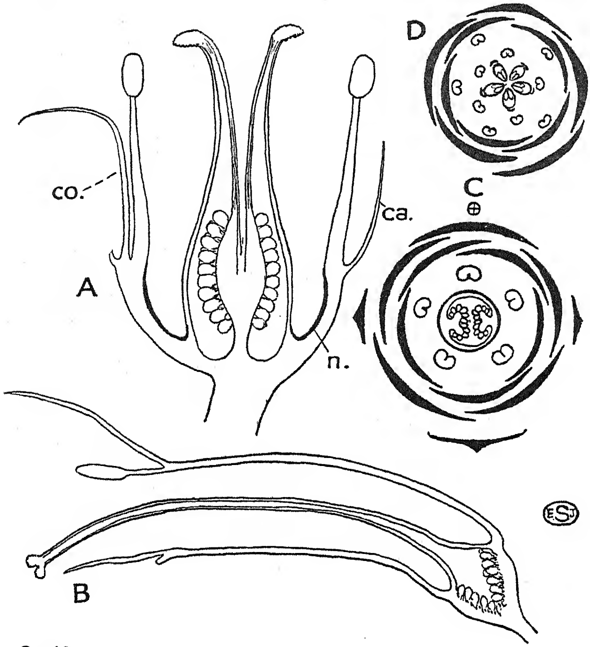

FIG. 425. Saxifragaceæ and Crassulaceæ. A, Longitudinal section of flower of *Saxifraga cordifolia*, showing perigyny. B, Ditto of *Ribes aureum*. C, Floral diagram of *Saxifraga*. D, Floral diagram of *Sedum*. *ca.*, calyx; *co.*, corolla; *n.*, nectary.

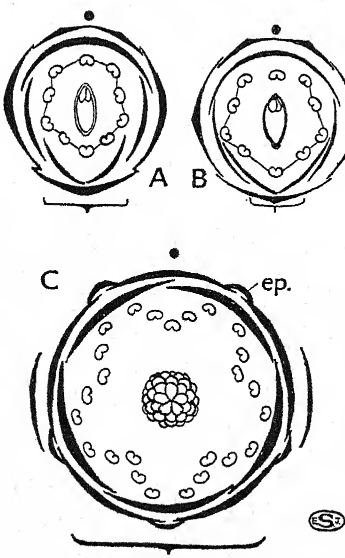

FIG. 426. A–B, Leguminosæ. C, Rosaceæ. A, Floral diagram of *Genista anglica*, B, of *Lathyrus odoratus*. C, Floral diagram of *Potentilla reptans*. *ep.*, epicalyx.

C papilionaceous (cf. p. 456); sta. joined by their filaments to form a tube (Fig. 426, A), or the posterior one free (Fig. 426, B); ov. usually pod-like, enclosed in sta.-tube, with ovules parietal on ventral suture. Fruit a legume (Fig. 333, *c*). All entom., visited mainly by Bees.

The commoner British genera which all belong to the subdivision *Papilionaceæ* are: *Anthyllis* (Kidney-vetch), with inflated hairy calyx; *Cytisus* (Broom), all 10 sta. joined, pollen flrs. (Fig. 320, A and B); *Genista* (Needle Furze), all 10 sta. joined, pollen-flrs. (Fig. 426, A); *Lathyrus* (Sweet-pea) (Fig. 320, C–E; 426, B); *Lotus* (Bird's-foot Trefoil) (Fig. 321) with piston-mechanism; *Medicago* (Medick), with spirally coiled legumes, frequently provided with hooks for animal-distribution, often indehiscent; *Melilotus* (Melilot), with keel-petals free from one another; *Ononis* (Rest-harrow), all 10 sta. joined; *Trifolium* (Clover), with flrs. in racemose heads (Fig. 319) and trifoliate leaves; *Ulex* (Furze or Gorse); *Vicia* (Vetch).

In the following genera the fruit is a lomentum which breaks up at maturity into one-seeded parts: *Hippocrepis* (Horseshoe-vetch); *Onobrychis* (Sainfoin); *Ornithopus* (Bird's-foot).

Amongst foreign representatives are: *Phaseolus* (Runner Bean); *Pisum* (Pea); *Vicia faba* (Broad Bean). Others, although possessed of papilionaceous flrs., have 10 free sta., e.g. *Cercis* (Judas tree), whilst still others have reg. flrs. which are densely grouped and have fewer stas. (*Mimosa*) or have ∞ conspicuous sta. (*Acacia*).

15. GERANIACEÆ (GERANIALES)

Herbs, often with aromatic foliage, leaves alt. Infl. cymose. Flrs. (Fig. 427, A) reg., K5 C5 A5 + 5 G(5), outer sta. opp. petals, usually one ovule in each loculus. Fruits schizocarpic.

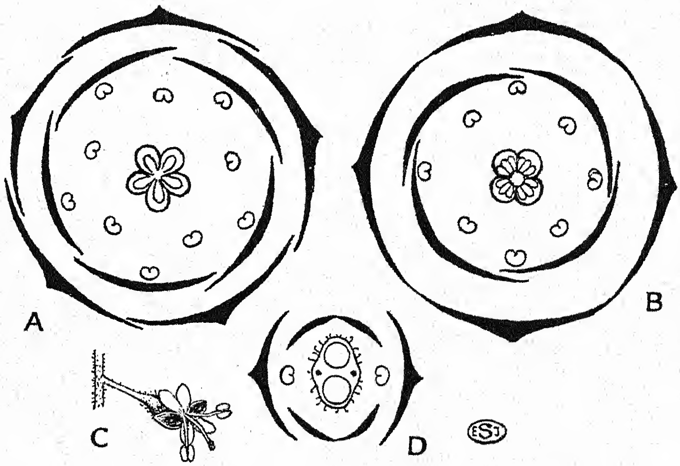

FIG. 427. Geraniaceæ and Onagraceæ. A, Floral diagram of *Geranium*. B, Floral diagram of *Epilobium*. C, Flower of *Circæa*. D, Floral diagram of same.

The chief British genera are: *Erodium* (Stork's Bill), with 5 sta. and 5 staminodes (p. 437); *Geranium* (Fig. 427, A), with 10 sta. The exotic *Pelar-*

gonium (Garden Geranium) has a slightly zygomorphic flr., with a spur concealed by fusion with the peduncle.

In the allied LINACEÆ (*Linum*, Flax), each cpl. contains two ovules, and there are 10 loculi in the ov., each with one ovule (p. 442).

16. ONAGRACEÆ (MYRTIFLORÆ)

Annual or perennial herbs, with opp. or alt. leaves. Infl. usually racemose. Flrs. dimerous (Fig. 427, C, D), or tetramerous (Fig. 311 and 427, B), ov. of 2–4 cpls., inf., 2–4 loculi with axile plac. and usually ∞ ovules, protandr. Fruit usually a capsule.

The common British genera are: *Circæa* (Enchanter's Nightshade, Fig. 427, C and D), with dimerous flrs. and hooked indehiscent fruit (Fig. 339, B); *Epilobium* (Willow-herb) and *Oenothera* (Evening Primrose) have tetramerous flrs. with 8 sta. (Fig. 311).

17. UMBELLIFERÆ (UMBELLIFLORÆ)

Mostly perennial herbs, with large, alt., exstip., usually cpd. leaves having big sheathing bases (Fig. 74, C); stem hollow and often ribbed (Fig. 87, A); tap-root generally prominent. Infl. usually a cpd. umbel, frequently with enlargement of the petals of the outermost flrs. Flrs. small, usually white or yellow, reg., ☿, epig., all parts except cpls. free, almost invariably with K5 C5 A5 G ($\bar{2}$) (Fig. 428, A, B). K very small, inconspicuous; petals often distant from one another; sta. 5, introrse; ov. inf., biloc., with 1 ovule in each compartment; stigma bilobed. Nectary as a disc on top of ov. (Fig. 428, B). Fruit a schizocarp (Fig. 334, A; 428, C, D); seeds end. Mostly protandr. and visited by Flies and Beetles. All parts of the plant usually contain aromatic oils, often of commercial value (*e.g.* Angelica, Aniseed, Caraway, etc.; cf. p. 90).

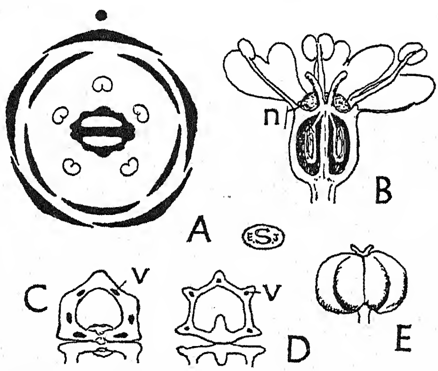

FIG. 428. Umbelliferæ. A, Floral diagram of *Heracleum*. B, Longitudinal section of flower of *Aethusa* (after Le Maout). C and D, Transverse sections of fruits of *Fœniculum* and *Conium*. E, Fruit of *Hydrocotyle*. *n.*, Nectary. *v*, Oil ducts.

The following are some of the commoner British genera: *Aegopodium* (Bishop's-weed); *Anthriscus* (Beaked Parsley), a spring hedge-plant; *Bupleurum*, with simple entire leaves; *Carum* (Caraway, Parsley); *Conopodium* (Pig-nut), with a tuberous root-stock, common in woods and meadows; *Crithmum* (Rock-samphire), found on rocky coasts, with fleshy leaves; *Daucus* (Carrot), with a tuberous root and spiny fruits; *Eryngium* (Sea-holly), a sand-dune plant, with palmately lobed spinous leaves and cymose capitula of blue flrs.; *Fœniculum* (Fennel), used in flavouring; *Heracleum* (Hogweed), common hedge-plant (Fig. 428, A, B); *Hydrocotyle* (Marsh Pennywort), with peltate leaves (Fig.428, E); *Oenanthe* (Water Dropwort), marsh- or water-plants;

Peucedanum (Parsnip), with a tuberous root, the wild form characteristic of chalk-pastures; *Sanicula* (Wood Sanicle), with flrs. in cymose umbels, simple palmately lobed leaves, and fruits with hooked spines; *Scandix* (Shepherd's Needle), a common weed of cultivated ground, with much elongated fruits.

The following are very poisonous: Fool's Parsley (*Aethusa*), a garden-weed; Wild Celery (*Apium*), the form used commercially having been rendered harmless under cultivation; Water Hemlock (*Cicuta*), a marsh-plant; Hemlock (*Conium*).

The ARALIACEÆ (including the Ivy, *Hedera*), and the CORNACEÆ (including Dogwood, *Cornus*) belong to the same Cohort Umbellifloræ.

(*b*) Sympetalæ (Families 18–32)

Parts of C fused, sta. generally few and epipetalous.

18. ERICACEÆ (ERICALES)

Small shrubs or trees, with alt. small evergreen leaves (Fig. 373), xeromorphic in habit. Infl. usually racemose. Flrs. (Fig. 299, B) usually with K4–5 C(4–5) A 4 + 4 or 5 + 5 G($\underline{4\text{–}5}$); outer sta. opp. petals; sta. with dehiscence by terminal slits or pores and often with appendages (Fig. 301, E), pollen in tetrads (p. 438); ovules usually several in each loculus, sometimes one; nectary round base of ovary. Fruit capsular or a berry.

The common British genera are: *Calluna* (Ling, Heather), with a deeply cleft 4-partite C and a loculicidal capsule; *Erica* (Heath, Fig. 373), with urn-shaped C (Fig. 299, B) and septicidal capsule; *Pyrola* (Wintergreen), evergreen, humus-loving plants, with one whorl of 5 sta.; *Vaccinium* (Bilberry, Whortleberry, Cranberry, Cowberry), fruit a berry. *Rhododendron* and *Azalea* are members of this family.

19. PRIMULACEÆ (PRIMULALES)

Annual or perennial herbs, with generally simple, alt., exstip. leaves, often radical. Infl. a raceme or umbel, or with solitary flrs. Flrs. reg., ☿, hypog., pentamerous, usually with K(5) C(5) A5 G($\underline{5}$) (Fig. 429). Corolla-tube often long, but very short in *Anagallis* and *Lysimachia*; sta. opp. the petals and epipetalous; ov. sup. (half-inferior in *Samolus*), uniloc., with free central plac. bearing ∞ ovules (Fig. 318); stigma capitate (p. 441). Nectar often formed at base of ovary. Fruit a capsule opening by teeth or lid; seeds end. Mostly entom., occasionally showing heterostyly (p. 455).

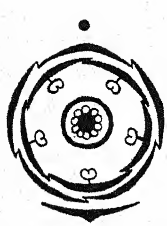

Fig. 429. Floral diagram of Primulaceæ (*Primula*).

The British genera are: *Anagallis* (Scarlet Pimpernel) and *Centunculus*, a rare plant found in inundated places, have capsules dehiscing by a lid; *Glaux* (Sea Milkwort), a succulent maritime plant, apetalous, self-pollinated; *Hottonia* (Water-Violet), heterostylic; *Lysimachia* (Creeping Jenny, Yellow Pimpernel, Loosestrife), some sp. heterostylic, some with staminodes alt. with the sta.; *Primula* (Cowslip, Oxlip, Primrose) (Fig. 318) with heterostylic flrs.; *Samolus* (Brookweed), a marsh-plant, with staminodes alt. with the sta. and bracts borne half-way up the peduncles; *Trientalis* (Wintergreen), northern plant with more than five petals.

20. GENTIANACEÆ (CONTORTÆ)

Herbs, usually with opp. entire exstip. leaves. Infl. often a dichasial cyme. Flrs. usually K(4–5) C(4–5) A4–5 $G(\underline{2})$; petals twisted (Fig. 300, A, C); ov. uniloc. with parietal plac. and ∞ ovules. Fruit a capsule.

The common British genera are: *Chlora* (Yellow Centaury), C and A 6–8, leaves connate; *Erythræa* (Centaury), with 5 sta., both genera with inwardly projecting placentæ; *Gentiana* (Gentian, Fellwort), with 4- or 5-merous flrs., placentæ not projecting; *Menyanthes* (Bog bean), marsh-plant with trifoliate alt. leaves and petals bearing ∞ fleshy white protuberances.

21. CONVOLVULACEÆ (TUBIFLORÆ)

Climbing herbs with alt. exstip. leaves, frequently with a watery latex. Flrs. reg., K5 C(5) A5 $G(\underline{2})$; C often trumpet-shaped (Fig. 299, C); ov. with axile placentæ and 2 ovules in each loculus. Fruit a capsule.

British genera: *Convolvulus* and *Cuscuta* (Dodder, p. 214; Fig. 129, 130).

22. SCROPHULARIACEÆ (TUBIFLORÆ)

Annual or perennial herbs, with alt. or opp., exstip., often hairy leaves. Infl. racemose or cymose. Flrs. usually irreg., ☿, hypog., generally with K(5) C(5) A4 $G(\underline{2})$ (Fig. 430, C). K gamosepalous, mostly irreg.; C various; sta.

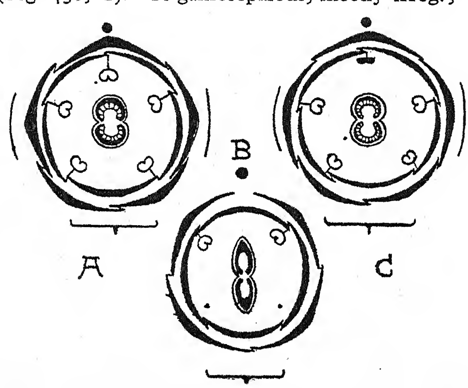

FIG. 430. Floral diagrams of Scrophulariaceæ. A, *Verbascum*. B, *Veronica*. C, *Scrophularia*.

usually 4, didynamous; ov. sup., bicarp., biloc., with swollen axile placs. bearing ∞ ovules (Fig. 323, D); stigma bilobed (Fig. 171, A). Nectar formed in a disc beneath the ov. Fruit a capsule; seeds end. All entom., mostly protandr. Many poisonous.

The principal British genera are: *Antirrhinum* (Snapdragon) (Fig. 323), with a closed corolla; *Digitalis* (Foxglove), with alt. leaves and irreg. tubular corolla (Fig. 299, E), poisonous; *Lathræa* (Toothwort, p. 215, Fig. 131); *Linaria* (Toadflax), with a closed corolla and a spur (p. 460); *Mimulus* (Musk), a river-side plant, with stigma sensitive to touch (p. 266); *Scrophularia* (Figwort), with opp. leaves and square stems and posterior staminode (Fig. 310 and 430, C), partial infl. a dichasial cyme; *Verbascum* (Mullein), with 5 sta. with very hairy filaments, and almost reg. flrs. (Fig. 430, A); *Veronica* (Speedwell),

with almost reg. flrs. having K4 C4 (posterior petal larger than the others) A2 G(2) (Fig. 430, B).

The following are all meadow-plants and semi-parasites (p. 530); Red Eye-bright (*Bartsia*), Fig. 372; Eye-bright (*Euphrasia*); Cow-wheat (*Melampyrum*); Red Rattles or Louseworts (*Pedicularis*); Yellow Rattle (*Rhinanthus*).

23. SOLANACEÆ (TUBIFLORÆ)

Mostly herbs with alt., sometimes cpd. leaves, and internal phloem. Infl. cymose, with frequent fusion of bract with axis resulting in displacement (Fig. 431, D and E). Flrs. (Fig. 431, A, B) often reg., with K(5) C(5) A5 G(2),

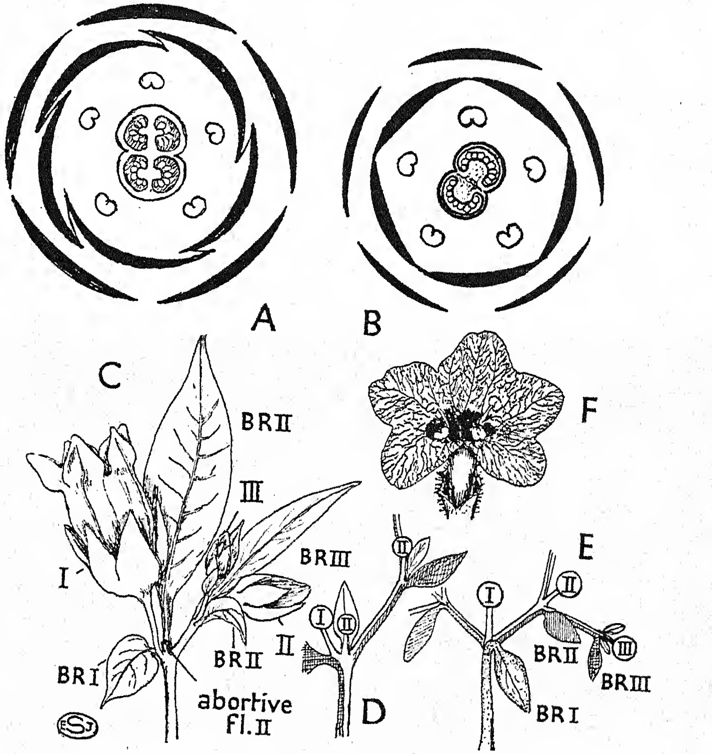

FIG. 431. Solanaceæ. Floral diagrams of *Datura* (A) and *Solanum* (B). C, Part of inflorescence of Deadly Nightshade (*Atropa belladonna*) to show mode of branching, represented by a diagram in D. E, Diagram of inflorescence of *Datura stramonium*. F, Single flower of Henbane (*Hyoscyamus niger*) to show zygomorphic corolla.

usually protog.; ov. biloc., axile plac., septum usually oblique to median plane (Fig. 431, B). Fruit usually a berry (Fig. 335, C, D). Many are poisonous.

The principal British genera are: *Atropa* (Deadly Nightshade, Fig. 431, C), with bell-shaped C and sta. dehiscing by slits; *Hyoscyamus* (Henbane, Fig. 431,

F), fruit a capsule opening by a lid; *Solanum* (Bittersweet, Woody Nightshade, Fig. 431, B), sta. with porous dehiscence.

Exotic sp. of *Solanum* include the Potato (*S. tuberosum*) and the Tomato (S. *lycopersicum*), the cultivated varieties of which often possess more than 2 cpls. *Datura stramonium* (Thornapple) (Fig. 49 and 431, A) is an important medicinal plant, with lobed plac.

24. LABIATÆ (TUBIFLORÆ)

Annual or perennial herbs, with opp., exstip., often hairy and glandular leaves; square hollow stems (Fig. 70, C and 87, B), swollen at the nodes. Infl. primarily racemose, but axillary flr.-clusters are dichasia (cf. p. 428). Flrs. irreg., ☿ (occasionally unisex.), hypog., usually with K(5) C(5) A4 G($\underline{2}$) (Fig. 432). K persistent, generally with 5 prominent teeth, often slightly irreg. (Fig. 297, C); C bilabiate (Fig. 299, D); sta. usually didynamous, beneath upper lip of corolla; ov. quadriloc., each loculus with 1 ovule; stigma bilobed. Nectar produced by a disc at base of ov., or restricted to its anterior side. Fruit schizocarpic of 4 achenes (Fig. 334, D); seeds end. All entom. and mostly protandr. Leaves often forming aromatic oils (*e.g.* Lavender, Rosemary, Marjoram; cf. pp. 90, 161).

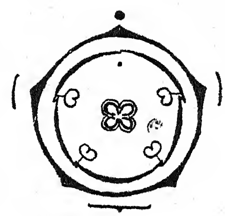

FIG. 432. Floral diagram of Labiatæ (*Lamium*).

British genera with 4 sta. of almost equal length are: *Mentha* (Mint); *Origanum* (Marjoram), a characteristic plant of chalk; and *Thymus* (*Thyme*). All three have only slightly irreg. C.

British genera which have 2 long and 2 short sta. are: *Ajuga* (Bugle), with a small upper lip; *Galeobdolon* (Yellow Deadnettle); *Galeopsis* (Hemp-nettle); *Lamium* (Deadnettle); *Nepeta* (Ground Ivy, Cat-mint) (Fig. 7), with the two upper sta. the longer; *Prunella* (Self-heal); *Scutellaria* (Skull-cap), with two lipped K, the upper lip pouch-like; *Stachys* (Woundwort); *Teucrium* (Wood Sage), with minute upper lip. The following have a specialised androecium: *Lycopus* (Gipsy-wort), with 2 perfect and 2 imperfect sta.; *Salvia* (Sage), with 2 fertile sta. only (Fig. 322).

25. BORAGINACEÆ (TUBIFLORÆ)

Annual or perennial herbs with bristly hairs. Infl. cymose, often coiled in the younger parts. Flrs. (Fig. 433, A) usually reg., K(5) C(5) A5 G($\underline{2}$). K persistent around fruit, which is schizocarpic of 4 achenes (Fig. 431, D), as in Labiatæ.

The common British genera are: *Anchusa* (Fig. 433, A); *Borago* (Borage), with projecting sta.; *Lithospermum* (Gromwell), with very hard whitish fruits; *Myosotis* (Forget-me-not); *Symphytum* (Comfrey), with bell-shaped C. All these have small scales in the throat of the C. *Echium* (Viper's Bugloss), with irreg. C and projecting sta., lacks such scales. The flrs. of *Pulmonaria* are heterostylic. To this family belongs the garden Heliotrope.

26. LENTIBULARIACEÆ (TUBIFLORÆ)

Insectivorous marsh or aquatic herbs, leaves alt. Infl. racemose or solitary. Flrs. irreg. (Fig. 433, B, C), K(3); C (5), 2-lipped; A2, anthers unilocular; G($\underline{2}$), ov. uniloc. with free central plac. (Fig. 433, B). Fruit a capsule. end. O.

The British genera are: *Pinguicula* (Butterwort) (Fig. 135); *Utricularia* (Bladderwort) (Fig. 137).

27. PLANTAGINACEÆ (PLANTAGINALES)

Herbs with radical rosettes. Infl. a spike (Fig. 313). Flrs. reg., anem., K(4) C(4) A4 G(2); C chaffy; sta. with long filaments attached at middle of anther; ov. with 2–4 loculi, axile plac. Fruit a capsule dehiscing by a lid (Fig. 333, *g*).

The British genera are: *Plantago* (Plantain), with ☿ flrs.; *Littorella* (Shoreweed), aquatic, with unisex. flrs.

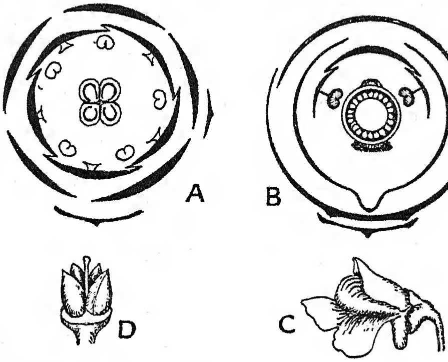

FIG. 433. Boraginaceæ and Lentibulariaceæ. A, Floral diagram of *Anchusa*. B, Floral diagram of *Utricularia*. C, Single flower of *Utricularia*. D, Fruit of *Myosotis*.

28. RUBIACEÆ (RUBIALES)

A family represented in Britain only by one tribe whose characters are: Herbs, with opp. leaves and stips. simulating whorls (4–10 at a node) (cf. p. 128). Infl. cymose. Flrs. (Fig. 434, A and H), reg., K(0–6) C(4–5) A4–5 G($\bar{2}$); ov. biloc., with 1 ovule in each loculus. Fruit generally schizocarpic.

The British genera are: *Asperula* (Woodruff, Fig. 434, A), woodland herb; *Galium* (Bedstraw, Cleavers, Fig. 8), with white or yellow flrs.; *Rubia* (Madder, Fig. 434, H), hedge-plant with leathery leaves, greenish flrs. and fleshy fruit. All these have only a vestigial K. *Sherardia* (Field Madder), with mauve flrs., has a well-defined K.

29. CAPRIFOLIACEÆ (RUBIALES)

Shrubs and herbs, usually with opp. stip. or exstip. leaves. Infl. usually a corymbose cyme. Flrs. (Fig. 434, B–G) reg. or irreg., K(5) C(5) A5 G($\overline{2–5}$), ov. with 1 ovule in each loculus, often uniloc. by abortion (Fig. 434, D). Fruit usually a berry or drupe.

The common British genera are: *Adoxa* (Moschatel), small woodland herb with alternate leaves and greenish flrs. in 5-flowered heads; *Lonicera* (Honeysuckle), with irreg. flrs. (Fig. 327 and Fig. 434, B); *Sambucus* (Elder), leaves pinnate, stip., stamens extrorse (Fig. 434, F); *Viburnum* (Guelder Rose, Wayfaring tree, Fig. 434, D and G), with simple leaves (Fig. 75, A) and drupes. The cultivated shrub *Diervilla* has capsular fruits. The Snowball Tree (*Symphoricarpus*) has white fruits with two fertile and two abortive loculi (Fig. 434, E).

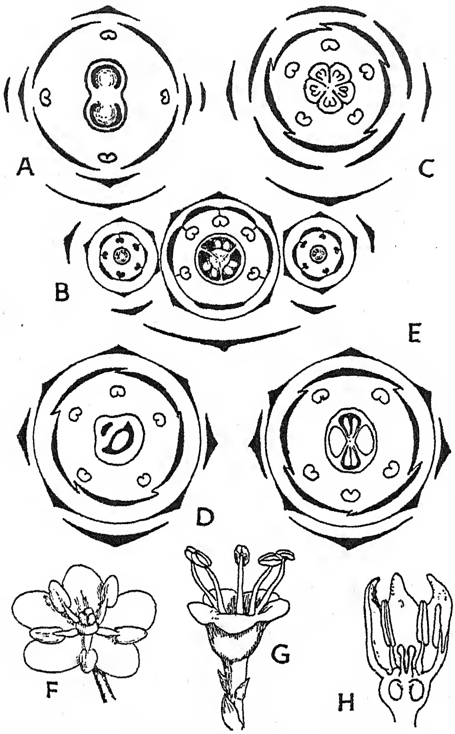

FIG. 434. Rubiaceæ and Caprifoliaceæ. A, Floral diagram of *Asperula.* B, Diagram of partial inflorescence of *Lonicera.* C, Floral diagram of *Leycesteria.* D, The same of *Viburnum opulus.* E, The same of *Symphoricarpus.* F, Flower of *Sambucus*, showing extrorse, and G, of *Viburnum opulus*, showing introrse stamens. H, Longitudinal section of flower of *Rubia peregrina.*

30. COMPOSITÆ (CAMPANULATÆ)

Annual or perennial herbs, with usually alt., exstip. leaves, often hairy. Infl. a capitulum, with an involucre of bracts, composed either of disc- and ray-florets (Fig. 312, A), or of ligulate florets only (Fig. 435, A), or of tubular ones only. Flrs. rarely with bracts, frequently yellow, reg. or irreg., ☿ or unisex., epig., usually with Ko C(5) A(5) G($\bar{2}$) (Fig. 435, C). K usually absent or represented by a pappus (p. 433); petals joined to form a tube or a ligulate structure (Fig. 297, E and 435, A); sta. syngenesious, introrse; ov. uniloc., with 1 basal ovule; stigma bilobed. Nectary ring-shaped round base of style. Fruit an achene, with pericarp and testa joined (p. 474), surmounted by the pappus. Mostly entom. and protandr. (cf. p. 462). A considerable number are common weeds.

The family is subdivided into:—

(i) *Tubulifloræ*:—Disc-florets tubular; no latex. The chief British genera are *Achillea* (Milfoil), with few-flowered capitula densely aggregated into corymbs, no pappus; *Anthemis* (Mayweed), cornfield-weeds, with bracts to

individual flrs.; *Aster* (Michaelmas Daisy), the British sp. maritime with fleshy leaves; *Bellis* (Daisy), no pappus; *Bidens* (Burr Marigold), marsh-plant, with opp. leaves and barbed bristles replacing pappus (Fig. 339, C); *Chrysanthemum* (Dog-daisy); *Erigeron* (Fleabane), a chalk-plant; *Inula* (Ploughman's Spikenard, Elecampane); *Matricaria* (Chamomile), cornfield-weeds; *Pulicaria* (Fleabane); *Senecio* (Groundsel, Ragwort); *Solidago* (Golden Rod); *Tussilago* (Coltsfoot), solitary capitulum appearing before the leaves, and having unisex. flrs. only (p. 449).

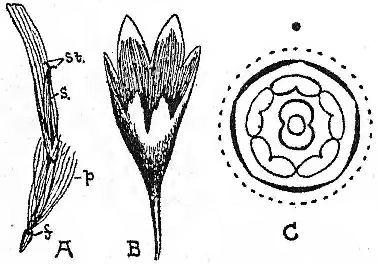

FIG. 435. A, Strap-shaped hermaphrodite floret of Dandelion (enlarged). *f*, ovary; *p*, pappus; *s*, stamen-tube; *st.*, stigma. B, Neuter floret of Cornflower (enlarged). C, Floral diagram of hermaphrodite floret of Compositæ.

The following genera of Tubulifloræ have only tubular flrs. in their capitula: *Antennaria*, with diœcious capitula; *Arctium* (Burdock), fruits with hooks on involucre (p. 483); *Artemisia* (Mugwort, Absinth, Wormwood), maritime or hedge-plants; *Carduus*, *Cnicus* (Thistles); *Centaurea* (Hardheads, Cornflower), with neuter outer flrs. (Fig. 435, B), irritable sta., and fringed bracts to involucre; *Eupatorium* (Hemp Agrimony), a marsh-plant with opp. leaves; *Filago* (Cudweed), with dense covering of white hairs; *Tanacetum* (Tansy), used medicinally.

(ii) *Ligulifloræ*:—All florets ligulate (Fig. 435, A); latex present. The more important British genera are: *Cichorium* (Chicory), with blue flrs.; *Hieracium* (Hawkweed) (p. 472); *Hypochœris* (Cat's-ear), with scaly bracts to individual flrs.; *Lactuca* (Lettuce); *Lapsana* (Nipplewort), common garden-weed, without a pappus; *Sonchus* (Sow-thistle); *Taraxacum* (Dandelion); *Tragopogon* (John-go-to-bed-at-noon, Salsify), with tuberous root, narrow grass-like leaves, and long bracts.

The following Compositæ are often cultivated: Artichoke and Cardoon (*Cynara*), young capitula of former used as a vegetable; *Dahlia*, with tuberous roots; Sunflower, Jerusalem Artichoke (*Helianthus*); *Scorzonera*, a vegetable with tuberous root.

31. CAMPANULACEÆ (CAMPANULATÆ)

Herbs with alt. exstip. leaves and usually possessing latex. Infl. racemose. Flrs. (Fig. 436, A, B, E), reg. or irreg., protandr., K5 C(5) A5 or (5) G($\overline{2}$–$\overline{5}$); sta. sometimes syngenesious; ov. 2–5-locular, with axile plac. Nectary round base of style. Fruit a capsule (pp. 476, 480).

The commoner British genera are: *Campanula* (Harebell, Canterbury Bell, Fig. 299, A, and 436, A and B); *Jasione* (Sheep's Bit), infl. a cymose capitulum, sta. syngenesious, 2 cpl. (Fig. 436, E); *Lobelia*, flrs. irreg., sta. forming a tube, the commoner of the two British sp. a submerged aquatic; *Specularia* (Venus' Looking-glass), with pod-like capsule and shining elliptical seeds.

32. DIPSACEÆ (AGGREGATÆ)

Herbs with alt. or opp. exstip. leaves. Infl. a cymose capitulum. Flrs. (Fig. 436, C and D) slightly irreg., protandr., K5 C(5) A4 G($\overline{2}$); K with epicalyx; sta. free; ov. uniloc. with 1 pendulous ovule. Nectary at base of style. Fruit an achene.

The British genera are: *Dipsacus* (Teasel), with connate leaves and conical capitula, order of flowering from the middle upwards and downwards; *Scabiosa* (Scabious), often with deeply lobed leaves, K bristly (Fig. 436, C and D).

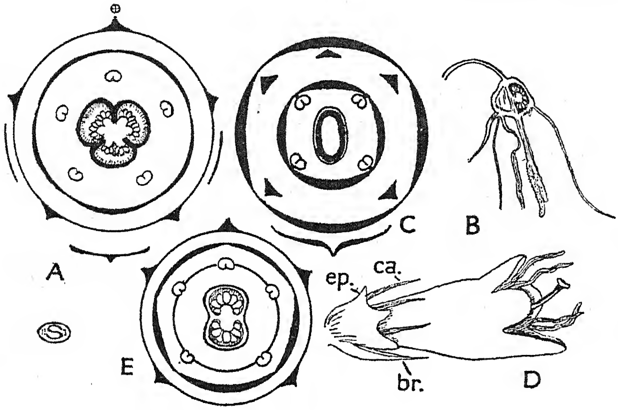

FIG. 436. Dipsaceæ and Campanulaceæ. A, Floral diagram, and B, Longitudinal section of flower of *Campanula*. C, Floral diagram, and D, Flower of *Scabiosa succisa*. E, Floral diagram of *Jasione*, showing joined anthers. *br.*, bract; *ca.*, calyx; *ep.*, epicalyx.

B. MONOCOTYLEDONS

33. LILIACEÆ (LILIIFLORÆ)

Perennial herbs, with underground rhizomes or bulbs, and sheathing lanceolate leaves, often radical. Infl. various, commonly a raceme. Flrs. reg., ☿, hypog., generally with P3 + 3 A3 + 3 G(3) (Fig. 437, A). P generally petaloid, free or joined; sta. occasionally epipetalous; ov. triloc., with axile placs., usually bearing ∞ ovules. Nectar often formed in ovary-wall (p. 452). Fruit a berry or capsule; seeds end. Many early-flowering.

The chief British genera having berries are: *Asparagus*, with linear cladodes (Fig. 352); *Convallaria* (Lily of the Valley), and *Polygonatum* (Solomon's Seal), both woodland-plants with a gamopetalous perianth, the latter with leafy stems; *Paris* (Herb Paris), woodland calcicole, with an often tetramerous flr., and Fly-pollinated (p. 464); *Ruscus* (Butcher's Broom) (Fig. 353, B), flrs. unisex., the ♂ with 3 sta., the ♀ with a uniloc. ov.

The following British genera have capsules: *Allium* (Onion, Garlic), with a cymose umbel, flrs. often replaced by bulbils (p. 234); *Colchicum* (Meadow Saffron), with a corm and a very long corolla-tube, flrs. in autumn, fruits in spring when the leaves appear; *Lilium*, with anthers movable on tops of filaments; *Muscari* (Grape Hyacinth), with bell-shaped C; *Narthecium* (Bog Asphodel), marsh-plant with *Iris*-like leaves; *Ornithogalum* (Star of Bethlehem); *Scilla* (Wild Hyacinth); *Tulipa*.

To the Cohort Liliifloræ also belongs the family JUNCACEÆ. These are mostly perennial herbs, often with scale-leaves and photosynthetic stems (p. 506); flrs. inconspicuous, with P3 + 3 scaly, A3 + 3 G(3). Fruits capsular. The two British genera are: *Juncus* (Rush), with triloc. ov., axile plac. and ∞ ovules; *Luzula* (Woodrush), with uniloc. ov., parietal plac., and 3 ovules.

34. AMARYLLIDACEÆ (LILIIFLORÆ)

Perennial herbs, with bulbs (p. 233) and leaves like those of Liliaceæ. Infl. often a cymose umbel. Flrs. (Fig. 437, B), reg., generally with P3 + 3 A3 + 3

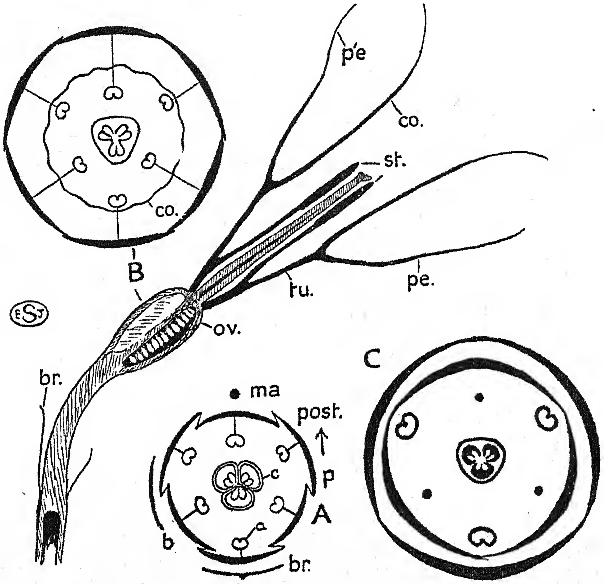

FIG. 437. A, Floral diagram of *Scilla* (Liliaceæ). *a.*, anther; *b.*, bracteole; *br.*, bract; *ma.*, inflorescence axis; *p.*, perianth. B, Floral diagram and longitudinal section of the flower of *Narcissus* (Amaryllidaceæ). *br.*, bract; *co.*, corona; *ov.*, ovary, showing loculus on one side and septum on the other; *pe.*, outer, and *p'e.*, inner perianth-segments; *st.*, stamen; *tu.*, tube; C, Floral diagram of *Crocus* (Iridaceæ).

G($\overline{3}$); P free or joined; sta. sometimes epipetalous; ov. triloc. with axile placs., bearing ∞ ovules. Fruit a capsule; seeds end. Chief difference from Liliaceæ lies in the epig. flr.

The British genera are: *Galanthus* (Snowdrop), flr. solitary; *Leucojum* (Snowflake); *Narcissus* (Daffodil), with long P-tube (Fig. 293, B, and Fig. 437, B).

35. IRIDACEÆ (LILIIFLORÆ)

Mostly perennial herbs, with rhizomes or corms and sword-shaped leaves arranged in two ranks and overlapping at the base. Infl. cymose. Flrs. (Fig. 437, C) ☿, similar to Liliaceæ, but with an inferior ov. and only 3 extrorse sta. belonging to the outer whorl. Fruit a capsule.

Of the British genera *Crocus* and *Sisyrinchium* (Blue-eyed Grass) have reg. flrs. In *Iris* the three styles are petaloid, a small ridge on the inner surface representing the stigmas; a sta. lies between each style and one of the outer petals, and biologically the flr. is comparable to three zygomorphic ones. *Gladiolus*, with one Brit. sp., and the commonly cultivated *Montbretia* have zygomorphic flrs. Most Iridaceæ are natives of S. Africa or Central America.

36. CYPERACEÆ (GLUMIFLORÆ)

Mostly perennial herbs with triangular aerial stems and Grass-like tristichous (p. 119) leaves, the leaf-base forming a closed sheath. Flrs. (Fig. 438) usually unisex. in spikes, P absent, or represented by bristles (Fig. 438, C), A usually 2–3, G($\underline{2–3}$), ov. uniloc. with 1 ovule, anem. Fruit an achene.

The common British genera are: *Carex* (Sedge), usually with ♂ and ♀ flrs.

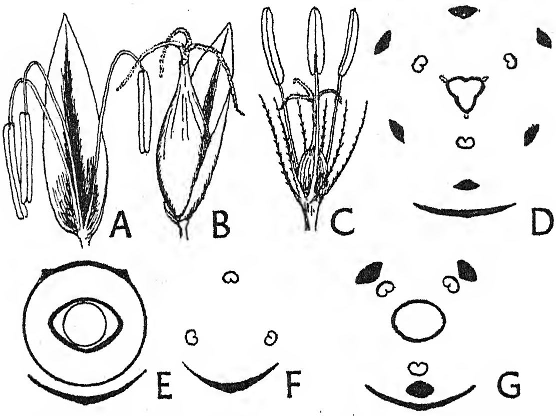

FIG. 438. Flowers and floral diagrams of Cyperaceæ. A, Male, and B, Female flowers of *Carex*. C, Flower, and D, Floral diagram of *Scirpus*. E and F, Floral diagrams of the female and male flowers of *Carex*. G, Floral diagram of *Eleocharis palustris*.

in separate spikes with conspicuous bracts, ♂ with 2–3 sta. (Fig. 438, A, F), ♀ with ov. of 2–3 cpls., surrounded by a protective sheath (Fig. 438, B, E); *Cladium*, characteristic of Norfolk fens; *Cyperus* (Galingale), with ☿ flrs. having a distinct P; *Eleocharis* (Club-rush, Fig. 438, G), cpls. 2–3, single terminal spikelet; *Eriophorum* (Cotton-grass), P bristles becoming long and silky in fruit; *Scirpus* (Bulrush), spikelets usually clustered and lateral, ☿ flrs. (Fig. 438, C and D).

37. GRAMINEÆ (GLUMIFLORÆ)

Annual or perennial herbs, with alt. distichous leaves having linear blades, long sheathing usually split bases, and ligules (p. 126 and Fig. 73, G); nodes swollen; stems commonly hollow and jointed; intercalary meristems above nodes (p. 258). Branching takes place freely from nodes (tillering), resulting in some sp. in tufted growth. Unit of infl. a *spikelet* (Fig. 439, A and B), *i.e.* a small group of 1–5 sessile flrs. borne on a very short axis, with a pair of bracts (*glumes*, Fig. 439, *l.g.* and *u.g.*) at the base, which more or less enclose the flrs.; spikelets arranged in cpd. inflrs. which are either cpd. spikes (e.g. *Triticum*) or cpd. racemes (e.g. *Avena*). Individual flrs. arising in axils of bracts (*flowering glumes*, Fig. 439, *f.g.*), the tips of which often form *awns* (Fig. 439, A, *a*); very low down on the peduncle each flr. bears a two-keeled bracteole (the *pale*, Fig. 439, *p*); the parts of the flr. till mature completely hidden between flowering glume and pale. Flrs. reg., ☿, hypog., generally with A3 G($\underline{2}$) (see Fig. 439, C). Between the sta. and the flowering glume two small

green fleshy outgrowths, the *lodicules* (Fig. 439, *ld.*), perhaps representing members of a reduced perianth. Sta. with long filaments and large, loosely hinged anthers (Fig. 439, A). Ov. with 1 ovule; stigma usually two-lobed and feathery (Fig. 439, A). Fruit an achene with pericarp and testa fused (p. 474); seed end., with embryo at one side (Fig. 17, I). Anem., mostly protog.

The principal British genera are: *Agropyron* (Wheat- or Couch-grass), with spikelets compressed at right angles to main axis; *Agrostis* (Bent-grass), with

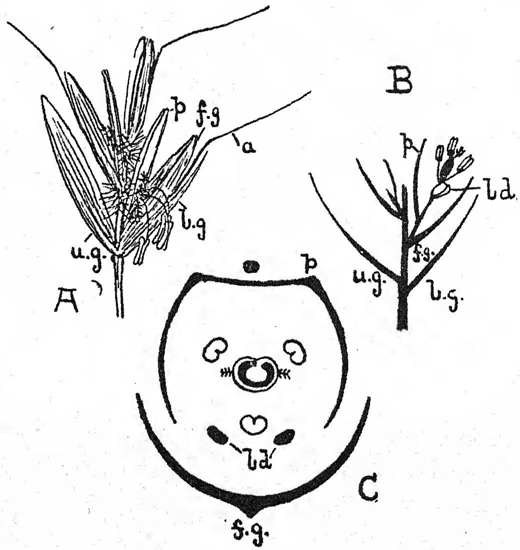

FIG. 439. Structure of spikelets and flowers of Grass (*Avena fatua*). A, Complete spikelet with parts spread out, containing three flowers, only one of which is open. B, Diagram of a spikelet with all parts of axis elongated. C, Floral diagram. *a*, awn; *f.g.*, flowering glume; *ld.*, lodicules; *l.g.*, lower glume; *p*, pale; *u.g.*, upper glume.

one-flowered spikelets; *Alopecurus* (Foxtail-grass), with a cylindrical compact infl.; *Anthoxanthum* (Sweet Vernal-grass), contains cumarin, flrs. with only 2 sta., lodicules absent; *Avena* (Oat), with long twisted awns (p. 483); *Brachypodium* (False Brome-grass), in woods, flrs. with 2 or 3 sta.; *Briza* (Quaking-grass), calciole, with ovate spikelets; *Bromus* (Brome-grass), with prominent awns; *Cynosurus* (Dog's-tail grass), on heaths, lower spikelets consisting only of glumes, the latter with a comb-like edge; *Dactylis* (Cock's-foot Grass), with all flrs. to one side, characteristic of meadows; *Aira* (Tussock-grass), on heaths, with two-flowered spikelets; *Elymus* (Lyme-grass), on sand-dunes; *Festuca* (Fescue), with many-flowered spikelets; *Glyceria* (Manna-grass), aquatic; *Holcus* (Soft-grass), with hairy leaves; *Hordeum* (Barley), with very long rough awns; *Lolium* (Rye-grass), in meadows, infl. flat with spikelets in 2 rows; *Melica* (Melic-grass), in woods, with one- to two-flowered spikelets and a single anterior lodicule; *Molinia* (Moor-grass), spikelets often purplish; *Nardus* (Mat-grass), on moors; *Phalaris*; *Phleum* (Cat's-tail Grass, Timothy-grass), with toothed flowering glumes and cylindrical infl.; *Phragmites* (Reed), swamp-plant, some-

times 16 ft., lower flrs. in each spikelet ♂; *Poa* (Meadow-grass), leaf-tip boat-shaped; *Psamma* (Marram-grass) (p. 562); *Spartina* (Cord-grass), on salt-marshes, with 2–3 very large stigmas.

Most Bamboos (*Bambusa*) have three lodicules and six stamens in two whorls. The Maize (*Zea*) has unisex. flrs. and the ♀ two fused stigmas.

Grasses are of great economic importance as cereals (see p. 75) and as fodder plants. The Sugar Cane (*Saccharum*), the Bamboos, and Esparto Grass are also important economically.

38. ORCHIDACEÆ (MICROSPERMÆ)

Perennial herbs, often with tuberous roots (p. 113), mostly with a mycorrhiza; leaves lanceolate or scaly, often radical. Infl. racemose, often a spike and frequently with coloured bracts. Flrs. irreg., ☿, epig., twisting through half a circle during their development (Fig. 326, B), generally with P3 + 3 A1 $G(\overline{3})$ (Fig. 440). P of 2 petaloid whorls, the posterior member (in mature flr. anterior in position) of the inner whorl enlarged to form the labellum (Fig. 326, A–C, *l*). Essential organs borne on a central column (Fig. 326, D, *c*) and generally consisting of 1 large sta. and a tricarp. ov. Sta. at top of column, with 2 prominent anther-lobes, each occupied by a pollinium (*p* in Fig. 326, D, see also p. 438) which is attached by a short stalk-like caudicle (*ca.*) to a pouch, the rostellum (*r*), above the stigmatic surfaces (*s*); 2 staminodes (*Std.*) often present on either side of the fertile sta.; ov. generally elongated and stalk-like (Fig. 326, B, *o*), uniloc., with 3 parietal placs. each bearing ∞ ovules; stigmatic surfaces 2, often more or less confluent. Labellum often prolonged into a spur (Fig. 326, B, *sp.*), at base of which the nectar is formed. Fruit a capsule with ∞ very minute seeds, end. O. Mostly entom. Many are found in woodlands, often on chalk-soils. All British sp. terrestrial.

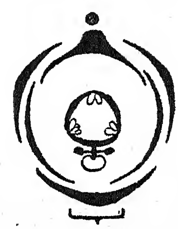

FIG. 440. Floral diagram of Orchidaceæ (*Orchis mascula*). The parts are shown in the positions which they occupy before twisting.

The family is subdivided into *Monandræ* (with only one fertile sta.) and *Diandræ* (with 2 fertile sta.), the former being mainly represented in Britain.

The principal British genera of *Monandræ* are: *Aceras* (Man-Orchis), with 4 pronounced lobes to labellum, no spur, green flrs.; *Corallorhiza* (Coral-root), a saprophyte; *Epipactis* (Helleborine), greenish-purple flrs., Wasp-pollinated; *Habenaria* (Butterfly-Orchis), Moth-pollinated, with night-scented white flrs. and long spurs containing free nectar; *Listera* (Twayblade), with 2 prominent leaves and greenish flrs.; *Neottia* (Bird's-nest Orchid) (Fig. 132, p. 218); *Ophrys* (Bee-Orchis, Fly-Orchis), flrs. without a spur and resembling various insects; *Orchis* (Fig. 326); *Spiranthes* (Lady's Tresses), with a twisted spike and fragrant white flrs.

The only member of *Diandræ* in Britain is *Cypripedium* (Lady's Slipper), with a large pouch-like labellum, 2 fertile sta., a large staminode, and a three-lobed stigmatic surface.

39. ALISMACEÆ (HELOBIEÆ)

Aquatic herbs, leaves mostly with a petiolate lamina and frequently with prominent apical hydathodes, often with latex-cells. Infl. often with whorled flrs. Flrs. (Fig. 441, B–E) ☿ or unisex., usually with K3 C3 A3 + 3 to ∞, $G\underline{6-\infty}$; ov. usually apocarp. Fruit an aggregate of achenes or follicles.

The chief British genera are: *Alisma* (Water Plantain), with $A3+3\ G\infty$, and achenes (Fig. 441, B and C); *Butomus* (Flowering Rush, sometimes placed

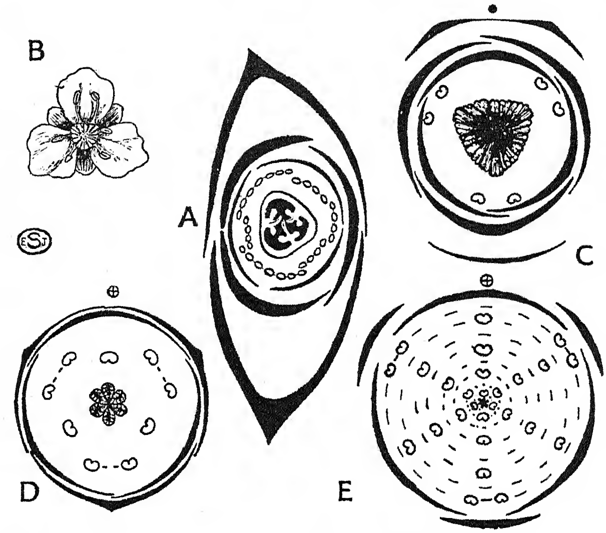

FIG. 441. A, Floral diagram of *Stratiotes* (Hydrocharitaceæ). B–E, Alismaceæ. B, Flower of *Alisma plantago*. C, Floral diagram of same. D, Floral diagram of *Butomus*. E, Floral diagram of male flower of *Sagittaria*. (After Salisbury.)

in a separate family), with $A6+3\ G\underline{6}$, and follicles (Fig. 441, D). These genera are ☿, but *Sagittaria* (Arrowhead, Fig. 387; Fig. 441, E) is unisex., with $A\infty\ G\infty$; fruits are achenes.

The HYDROCHARITACEÆ (*Hydrocharis*, *Stratiotes*) (Fig. 441, A) are closely allied to the Alismaceæ and chiefly distinguished by having an inf. ov.

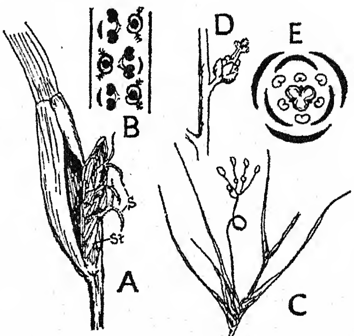

FIG. 442. A, Inflorescence and, B, Diagram of the male and female flowers of *Zostera*. C, *Ruppia*. D, Flower, and E, Floral diagram of *Triglochin palustre*.

40. POTAMOGETONACEÆ (HELOBIEÆ)

Mainly aquatics, with submerged and sometimes floating leaves having sheathing bases with scales on the inner surface. Infl. usually a spike (Fig. 291). Flrs. ☿ or unisex., P. absent or scale-like, A1–4 G$\underline{1\text{–}4}$; cpls. often joined at the extreme base, each with 1 ovule; anem. or hydrophilous. Fruit generally an achene.

The common British genera are: *Potamogeton* (Pondweed), A4 G4 (Fig. 291), achenes sessile; *Ruppia*, with stalked achenes (Fig. 442, C). These two genera have ☿ flrs., but *Zostera* (Eel-grass) has unisex. flrs. in the same infl. (Fig. 442, A and B). *Triglochin* (Arrow-grass) belongs to a closely allied family Juncaginaceæ, marsh-plants with Rush-like leaves, P3 + 3 A3 G($\underline{6}$), syncarp., all or only 3 cpls. fertile.

APPENDIX

I. *The Compound Microscope* (Fig. 443).[1]—This consists essentially of a stand which has for its purpose the appropriate support and adjustment of the optical parts. The latter comprise two systems of lenses, known respectively as *ocular* (*Oc.*) and *objective* (*Ob.*), whilst accessory structures are constituted by a mirror (*M.*) for reflecting light, and a *condenser* (*Co.*) for concentrating light upon the object.

The stand consists of a heavy *foot* or base (*Fo.*), bearing a rigid upright *pillar* (*L.*). To the latter the remaining portions of the microscope are hinged in such a way that the whole can be employed either in a vertical or in an inclined position. The part actually hinged to the pillar is known as the *limb*, and to this the flat *stage* (*S.*) is attached, at right angles, at the lower end, and the *body tube* (*T.*) towards the upper end. The stage, which is usually square, is perforated by a central aperture through which the light from the mirror reaches the object. In transferring the microscope from place to place, it should always be carried by the non-movable parts.

The body tube is a hollow brass cylinder and is adapted to take the *ocular* or *eyepiece* (*Oc.*) at its upper, and the *objectives* (*Ob.*) at its lower, end. In order to secure rapid change of magnification, a *nosepiece* (*N.*), bearing two or three objectives, is screwed into the lower end of the body tube; by simply turning this a different objective can be brought to bear on the object. The distance between eyepiece and objective can be increased or decreased by pulling out or pushing in the draw-tube (*D.t.*), which is fitted into the upper end of the body tube; the body tube length for which most objectives are corrected is 170 mm. In order to focus the object clearly, the entire system of lenses can be moved nearer to, or farther from, the stage by means either of the coarse or fine adjustments. The *coarse adjustment* usually consists of two large milled heads (*C.*) on either side of the limb, and by turning either of these, which actuate a rack and pinion mechanism, a relatively large movement is brought about. The *fine adjustment* is generally operated by a milled head (*F.*), situated at the top or side of the limb, and by this means a very slight movement is effected, enabling greater accuracy of focussing to be attained.

Below the stage is fixed an adjustable aperture, the *diaphragm* (*D.*), by means of which the amount of light reaching the object on the stage can be regulated. If a condenser is present, it is placed between the diaphragm and the stage, and, in the best instruments, its distance below the stage is adjustable by means of another milled head (*H.*). The mirror (*M.*), which is concave on one surface and flat on the other, is either attached to the under side of the stage or (as in the type illustrated) forms part of the adjustable system bearing the condenser.

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[1] See E. J. Spitta, *Microscopy*, J. Murray, 3rd edit., 1920 (537 pp.); J. Belling, *The Use of the Microscope*, McGraw Hill Book Co., 1930 (315 pp.).

The objectives most commonly in use are $\frac{2}{3}$ in. and $\frac{1}{6}$ in.,[1] which designations imply that, when focussed upon the object, they are approximately two-thirds and one-sixth inch respectively from the latter. These distances are the focal lengths, and the smaller they are the greater is the magnifying capacity of the lens. As a consequence, the longer focus lens is often spoken of as the *low power*, and the short focus lens as the *high power*. The image formed by the

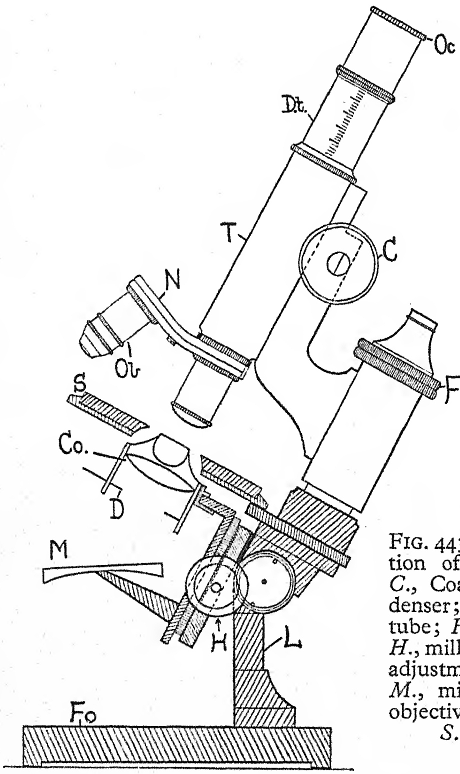

FIG. 443. Diagrammatic representation of a compound microscope. *C.*, Coarse adjustment; *Co.*, condenser; *D.*, diaphragm; *D.t.*, draw-tube; *F.*, fine adjustment; *Fo.*, foot; *H.*, milled head controlling substage adjustment for condenser; *L.*, pillar; *M.*, mirror; *N.*, nosepiece; *Ob.*, objective; *Oc.*, ocular or eyepiece; *S.*, stage; *T.*, body tube.

objective is projected on to the eyepiece, where it becomes further magnified. The amount of magnification of the eyepiece is commonly indicated by a number engraved upon it.

The object to be examined, mounted on a glass-slip in water or some other appropriate fluid and covered with a cover-glass, is placed on the stage, and light is projected on to it from below by means of the mirror. If a condenser is present, the flat side of the mirror is employed, but if not, the concave side. To focus the object, *gradually* lower the tube by means of the coarse adjustment till the image becomes clear, and then turn the milled head to and fro until the image appears most distinct. Proceed in the same way when

[1] For the study of Bacteria and other minute organisms, higher powers are required, such as $\frac{1}{12}$-in. oil immersion objectives, in which a small drop of cedar oil between objective and cover-glass forms part of the optical system.

using the high power, but exercise the greatest care not to bring the objective in contact with the cover-glass, and *immediately* the image *begins* to appear use the fine adjustment only. The aperture of the diaphragm should be diminished till the maximum amount of detail is visible, whilst by adjusting the condenser the light reflected from the mirror can be accurately focussed upon the object.

In working with the microscope, it is best to accustom oneself to employ either eye. When drawing, view the object with the left, and sketch with the aid of the right, eye. As a first exercise in microscopic observation, it is well to examine the small air-bubbles almost invariably present in large numbers in a drop of water. Under the low power these appear as black dots or bright patches with broad dark margins; this dark border is due to refraction. Adjust the slide so that one of the smaller bubbles is in the centre of the field of view, and turn the nosepiece so as to view the bubble with the high-power lens. Using the fine adjustment, it will be noted that at a high focus the curved surface is seen and the outline appears shadowy, whilst at a lower focus only the circular equatorial portion (the *optical section*) is visible, and the outline becomes well defined.

II. *Measurement under the Microscope.*—This is accomplished by means of an eyepiece micrometer and a stage micrometer (both obtainable from the usual dealers in microscopic requisites). The stage micrometer is an ordinary slide on which is mounted a scale of one millimetre, divided into tenths and hundredths, and obtained by photographic reduction. The eyepiece micrometer fits into the ocular, and consists of a scale that is usually divided into a hundred equal parts. For each objective the value of a division of the eyepiece micrometer is determined in terms of the divisions of the stage micrometer (*i.e.* in hundredths of a millimetre). If subsequently any object is measured with the eyepiece scale, its actual size can be calculated. The size of microscopic objects is measured in μ (= ·001 millimetre).

III. *Section-cutting.*—During this operation both razor and material should be kept moist with either water (for fresh material) or spirit (for preserved material). Hold the object between the thumb and first finger of the left hand, and arrange the tips of the remaining fingers so as to form a rest on which the razor blade can be glided backwards and forwards through the material. Note that the razor must be gently drawn through the object, and not pressed, as in ordinary cutting. The greatest care should be taken that the axis of the object is either at right angles (for transverse sections) or parallel to the razor blade (for longitudinal sections). For longitudinal sections only a very short length of the stem, etc., should be used. When very thin objects, such as leaves, are to be cut transversely, small rectangular pieces, including a vein, are embedded in a vertical incision made in a short length of Elder-pith, saturated with either water or spirit. Sections are then cut of the pith, as well as of the embedded object.

After cutting, transfer the sections to a slide, on which a drop of water or dilute glycerine has previously been placed, by means of a well-moistened brush, and reject all but the *two thinnest.* Complete sections are mostly quite unessential, whilst the small pieces will usually be the thinnest. Oblique sections, even if thin, are quite valueless. The razor should be carefully cleaned by wiping it from the back towards the edge.

IV. *Preserving and Staining.*—To preserve material for anatomical investigation, ordinary methylated spirit will usually serve, provided there is at least four times the volume of liquid as of material. For showing nuclear

structure, however, other fixatives are employed,[1] *e.g.* acetic alcohol, made by adding one part of glacial acetic acid to four parts of alcohol. After remaining in this for a few minutes up to several hours, according to the texture of the material, the latter is transferred to ordinary spirit.

For staining, the thinnest sections (cf. p. 632) should be placed in a few drops of safranin,[2] on a slide, for from five to fifteen minutes, more safranin being added at intervals to replace that lost by evaporation. The excess of the stain is now removed by washing the sections with spirit, and then a few drops of Kleinenberg's hæmatoxylin are allowed to act for half a minute. After this the sections are washed with spirit, and permanent preparations are made in the following way:—

The spirit is changed several times, finally using absolute alcohol. In this way dehydration (*i.e.* removal of water) is effected. To the alcohol a little clove oil is then added, and this mixture is in turn replaced by pure clove oil. The sections should now become transparent, and, if this fails to occur, they have not been sufficiently dehydrated. After two to three minutes the oil is poured off, and Canada balsam, dissolved in xylol, added. A cover-glass is then carefully let down on to the sections, and the slide placed on one side till the balsam sets. Throughout all these processes the greatest care should be taken that the sections are never without a covering of liquid.

If permanent preparations are not required, such stains as phloroglucin, aniline chloride, etc. (cf. Appendix V), can be employed to differentiate the tissues, and the sections are usually mounted in glycerine diluted with an equal volume of water. Preparations can also be mounted in glycerine jelly, such mounts being much more rapidly and easily prepared than those with Canada balsam, but they often perish after some years.

The liquid stains most commonly employed are prepared as follows:—

Aniline Blue.—Saturated solution in alcohol or water, with a trace of acetic acid.

Bismarck Brown.—Dissolve 2 grams in 100 c.c. of 70% alcohol. Stain for about $1\frac{1}{2}$ minutes.

Eosin.—1% solution in either water or alcohol. Stain for 3 to 5 minutes.

Gentian Violet.—1% solution in water. Stain for from 10 to 15 minutes, transfer to alcohol, and quickly counterstain with Bismarck brown.

Hæmatoxylin.—Best bought prepared ready for use.

Methylene Blue.—Saturated aqueous solution. For live staining this is greatly diluted.

Safranin.—1% solution in 50% alcohol.

V. *Reagents.*—Details as to the mode of preparation of the principal reagents mentioned in this book are given in the following:—

Ammoniated Copper Oxide (*Cuprammonia*).—This reagent must be freshly prepared. Add ammonium chloride, and subsequently excess of sodium hydrate, to a solution of copper sulphate. The blue precipitate produced is

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[1] See C. J. Chamberlain, *Methods in Plant Histology*, Univ. of Chicago Press, 5th edit., 1933 (416 pp.); H. J. Conn, *Biological Stains*, New York, 3rd edit., 1936 (276 pp.); A. B. Lee, *The Microtomist's Vademecum* (edited by G. J. B. Gatenby), J. A. Churchill, 10th edit., 1937 (784 pp.); G. J. B. Gatenby, *Biological Technique*, Churchill, 1937 (130 pp.), gives information on the theory of staining and other technical methods.

[2] Or methyl blue can be used, the sections being left in this for about half a minute.

filtered and washed thoroughly, and then dissolved in a small quantity of strong ammonia.

Aniline Sulphate.—Dissolve 0·1 gram in 10 c.c. of water and add a drop of sulphuric acid. The chloride is often used instead of the sulphate.

Chlor-zinc-iodide.—Dissolve an excess of zinc in pure hydrochloric acid and evaporate to the consistency of strong sulphuric acid; as much potassium iodide is added to the solution as it will dissolve and then as much iodine. In applying the test use sections mounted in water. The solution loses its properties after some weeks.

Eau de Javelle (mainly potassium hypochlorite).—Mix 20 parts of chloride of lime with 100 parts of water. Allow to stand, and then add a solution of 15 parts of caustic potash in 100 parts of water. Filter after some hours and use the filtrate.

Fehling's Solution (an alkaline solution of cupric oxide) (after Haas).—This is best obtained by mixing equal quantities of a solution containing 69·28 grams of pure crystallised copper sulphate in 1 litre, and of a solution containing 350 grams of Rochelle salt (sodium potassium tartrate) and 100 grams of sodium hydrate in 1 litre. The resulting solution is of a clear dark blue colour. Ten cubic centimetres of this solution are reduced by 0·05 gram of glucose.

Iodine Solution.—This is made by dissolving crystals of iodine in a strong solution of potassium iodide. For use this is diluted to a light brown colour. Tincture of iodine is a solution in alcohol.

Light Green.—This can be dissolved in water, alcohol, or clove oil. To make an alcoholic solution 1 gram is dissolved in 100 c.c. of alcohol.

Millon's Reagent.—This is a mixture of mercuric nitrate and nitrite. It can be prepared by dissolving 15 grams of mercury in 30 grams of cold nitric acid (sp. gr. 1·42), which operation should be performed in a fume cupboard. Dilute with twice the volume of distilled water, and filter after two hours. This reagent can also be bought ready made from the usual dealers in chemicals.

Phenylhydrazine Hydrochloride (after Mangham).—Prepare separate solutions, in ten times their weight of glycerine, of phenylhydrazine hydrochloride and sodium acetate respectively. Place the material to be investigated in equal drops of these two solutions, thoroughly mixed, and, after covering with a cover-glass, heat for one to several hours in an oven.

Phloroglucin.—Prepare a saturated solution in alcohol. Treat material with this for a short time, and then mount in strong hydrochloric acid.

Pyrogallate of Potash.—This is obtained by dissolving pyrogallic acid in water and adding an excess of caustic potash (which should not be done until immediately before the experiment is started). This solution absorbs oxygen very energetically, as a result of which it takes on a brown colour.

Scharlach Red.—Prepare a saturated solution in a mixture of 70 parts absolute alcohol and 30 parts water by volume. Filter and keep well stoppered.

Sulphuric Acid.—For cellulose tests it is usual to employ the concentrated acid. *Great care must be exercised in its use*, and strong ammonia should be at hand to neutralise any drops that may be spilled.

VI. *Artificial Sea-water.*—For this purpose Tidman's sea-salt, dissolved in distilled water in appropriate concentrations, can be employed; or a solution can be made according to the following formula given by Osterhout:—

1000	parts	sodium chloride (gram-molecular solution).
78	,,	magnesium chloride (gram-molecular solution).
38	,,	magnesium sulphate (gram-molecular solution).
22	,,	potassium chloride (gram-molecular solution).
10	,,	calcium chloride (gram-molecular solution).

This solution has an osmotic pressure of about 22·4 atmospheres; when diluted with an equal volume of distilled water, the osmotic pressure is halved, when diluted with twice its bulk of distilled water the osmotic pressure is one-third of that of the undiluted solution, and so on.

For the following data, which refers to strengths of Tidman's sea-salt, we are indebted to Dr. F. M. Haines:—

Concentration of solution in grams per 100 c.c.	Osmotic pressure in atmospheres.	Concentration of solution in grams per 100 c.c.	Osmotic pressure in atmospheres.
0·01	0·08	0·7	5·6
0·02	0·16	0·8	6·4
0·03	0·24	0·9	7·15
0·04	0·32	1·0	7·95
0·05	0·40	1·1	8·7
0·06	0·48	1·2	9·6
0·07	0·56	1·3	10·3
0·08	0·64	1·4	11·1
0·09	0·72	1·5	11·9
0·1	0·8	1·6	12·7
0·2	1·6	1·7	13·5
0·3	2·4	1·8	14·3
0·4	3·2	1·9	15·1
0·5	4·0	2·0	15·9
0·6	4·8		

The osmotic pressure for concentrations between those given in this table are proportional to the values between which the particular concentration lies.

VII. *Artificial Semi-permeable Membranes.*—The membranous precipitate of copper ferrocyanide can be deposited in celloidin or in the wall of a small pot of unglazed porous porcelain. The latter is thoroughly washed so that it is impregnated with water. It is then nearly filled with a dilute solution of copper sulphate (2·5 grams per litre) and stood in a solution of potassium ferrocyanide (2·1 grams per litre), where it is left for some time. Ultimately it is thoroughly washed and soaked in water. It is best to prepare several pots in this way, as some are sure to be faulty. To overcome this difficulty, Philip recommends depositing the copper ferrocyanide precipitate in a film of gelatine, formed over one end of a glass tube by dipping it in 20 per cent. gelatine to which a little potassium bichromate has been added; the latter has the effect of rendering the gelatine insoluble, if it is allowed to set in the light. After this the tube is again filled with the copper sulphate and the closed end allowed to dip into the potassium ferrocyanide solution until the gelatine has acquired the brown colour of the precipitate.

The membrane of celloidin can be obtained by pouring a solution of the latter on a clean mercury surface contained in a Petri dish and allowing the solvent to evaporate away. The membrane which remains is then fitted over the open end of a thistle funnel, the overlapping portion being tied securely round the flange of the bulb. In drying, the membrane contracts slightly and becomes stretched taut. A very strong combination is obtained if two membranes of this kind are fitted over one another.

A piece of pig's bladder, which should be thoroughly dried before use, stretched over the end of a thistle funnel, is often quite effective as a semi-permeable membrane.

VIII. *Analysis of Ash.*—The presence of a few of the elements can be detected very simply. Thus, if a clean platinum-wire be moistened with hydrochloric acid, dipped into the ash, and held in the non-luminous flame of a Bunsen burner, the yellow colour indicates the presence of sodium. If the flame is viewed through a piece of blue cobalt-glass, the violet colouration due to potassium is recognisable. If the ash is boiled with water, the filtrate, after being acidified with hydrochloric acid, gives a white precipitate with barium chloride, thus indicating the presence of sulphur in the form of sulphates. A portion of the filtrate treated with an equal amount of dilute nitric acid, followed by an excess of ammonium molybdate solution, gives on boiling a yellow precipitate due to the presence of phosphates.

IX. *Details of Water- and Sand-cultures.*—In place of water-cultures, sand-cultures may be prepared in the following way: A quantity of silver sand is strongly heated for some time and allowed to cool again. After this, boiling water is allowed to drain through it several times in succession. The sand is then placed in small pots which are watered daily with the different kinds of culture-solutions. For such experiments it is advisable to employ plants which readily grow in a sandy soil, such as Poppy or Cress.

If water-cultures are continued for some time, it is advisable to renew the culture-solution every few weeks. Should the roots begin to show a growth of Moulds or Bacteria, the latter should be carefully removed with a fine brush; to prevent a growth of this kind on the under sides of the corks, the latter should be charred. Large jars should be used for the experiments, whilst as regards plants Maize, Wheat, Sunflower, etc., give good results.

For solution without nitrogen, see p. 207. To make up one lacking sulphur, substitute magnesium nitrate for magnesium sulphate and calcium nitrate for calcium sulphate. To eliminate phosphorus, use ferric sulphate instead of ferric phosphate. For the solution without calcium, employ magnesium nitrate in place of calcium sulphate, and for the one without potassium, substitute sodium for the potassium salt.

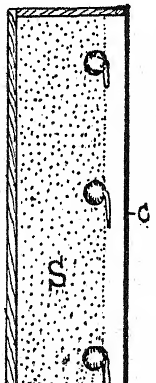

FIG. 444. Section of box to show method of growing seedlings with straight plumules and radicles. *S*, sand; *C*, cover of box.

X. *Method of obtaining Seedlings with Straight Radicles and Plumules* (Fig. 444).—A flat seed-box is filled with moist sand, in the surface of which are embedded rows of soaked seeds parallel to the long sides of the box. The seeds must be so placed that their radicles are all directed towards the same side and lie parallel to one another; about 2 inches should be left between the successive rows (Fig. 444). The box is covered, either with a sheet of cardboard or a piece of wood which is merely tied on, so as to be readily removed. The whole is then stood on one of its edges or suspended, vertically, with all the radicles pointing downwards. A very considerable proportion of the seeds will be found to develop straight radicles and plumules (Fig. 444).

XI. *Method of marking Radicles or Plumules with Indian Ink.*—The marking may be most conveniently carried out by using a piece of cotton, stretched on a short piece of bent fish-bone or other flexible material like an archer's

bow. The radicle or plumule is laid along the edge of a scale and the marks are made by the stretched cotton which is moistened with Indian ink.

XII. *Attachment of Rubber Tubing in an Air-tight Manner.*—The internal diameter of the tubing should be somewhat smaller than the diameter of the object to which it is to be attached. Moistening with water will make it easier to slip the tubing over the object. To ensure an air-tight connection, thin copper wire may be firmly twisted around the points of junction.

XIII. *Method of filling a Narrow Tube with Liquid* (Fig. 445, A).—A fine glass-tube is attached to a small funnel and inserted into the tube to be filled, so as to reach to its base. The liquid is then poured into the funnel and, as the wider tube fills, the narrower one is withdrawn.

XIV. *Method of passing a Branch through a Hole in a Rubber Cork* (after Osterhout, Fig. 445, B).—A cork-borer, wide enough to take the branch, is passed through the hole in the cork, in the opposite direction to that in which it is desired to insert the branch. The latter is pushed some little way into the borer (Fig. 445, B), which is then slowly withdrawn, thus leaving the branch in the cork.

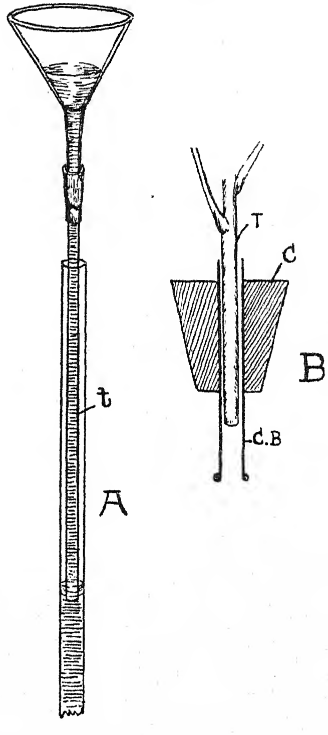

FIG. 445. A, Method of filling a narrow tube with liquid. *t*, glass-tube filled with water and attached to funnel. B, Method of passing a branch through a hole in a rubber cork (after Osterhout). *C*, cork; *C.B.*, cork-borer; *T*, shoot.

XV. *Graduation of Scale in Apparatus shown in Fig.* 154.—The apparatus is laid down horizontally, with the pointer at the base of the scale, and a centimetre scale is placed vertically (*i.e.* parallel to the support) against the end of the short arm of the lever. This latter is then moved through successive intervals and the corresponding positions of the pointer on the arc (*a*) marked off.

XVI. *Method of covering Leaves with Stencil-plates.*—The stencil-plate is placed on the upper side of the leaf, whilst a piece of cardboard of equal size and perforated by a number of small holes is fixed in a corresponding position on the lower surface. The two structures can be kept in position by fastening them with spiral paper-clips.

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*The principal references are printed in heavier type. Illustrations are indicated by an * after the paginal reference.*

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